

The Cretaceous echinoid *Boletechinus*, with notes on the phylogeny of the Glyphocyphidae and Temnopleuridae



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Synopsis

Boletechinus delawaricus sp. nov. from the Upper Cretaceous of Delaware, U.S.A. and *B. rowei* (Gregory) *anglicus* subsp. nov. from the Upper Cretaceous of England are described for the first time, and *Zeuglopleurus costulatus* Gregory, *Boletechinus rowei rowei* (Gregory) and *B. mcglameryae* Cooke are redescribed. The new family Zeuglopleuridae is erected to comprise *Zeuglopleurus*, *Boletechinus*, *Glyptocyphus*, and probably *Echinocyphus*. *Zeuglopleurus rowei* Gregory from the English Upper Cretaceous is referred to the genus *Boletechinus*, and one of the original syntypes of *Z. rowei* is made the holotype of the new subspecies *B. rowei anglicus*.

Introduction

The 'regular' echinoid *Boletechinus* has until now been recorded only from the Maastrichtian of Sumter County, Alabama where it is represented by one species, *B. mcglameryae*, described by C. Wythe Cooke in 1955. It was therefore interesting to receive from Mr R. Baker of Ramsgate, Kent, three specimens of *Boletechinus* from the Navesink Marl of the Delaware Canal, Delaware.

This paper describes the new species of *Boletechinus* from the Maastrichtian, Navesink Marl of Delaware, examines the English species of *Zeuglopleurus* and *Boletechinus*, and discusses their classification with respect to the Glyphocyphidae and the Temnopleuridae.

Relatively few echinoids have been described from the Upper Cretaceous of Delaware, whereas other types of fossil are well represented. C. Wythe Cooke (1958) opened his work by stating '... On the following pages are described all the echinoids known from the Upper Cretaceous deposits of the Atlantic Coastal Plain north of Virginia ...' and described twelve

species, of which only four 'irregular' echinoids are from Delaware. Of these four, *Faujasia geometrica* (Morton) and *Hardouinia florealis* (Morton) are probably from the Marshalltown Formation (Campanian). *Hemiaster delawarensis* Clark is probably from the Mount Laurel Sands (Campanian), while *H. ungula* Morton comes from an unknown formation. None of them are from the Navesink Marl of Delaware, but *Oolopygus williamsi* Clark comes from the Navesink Marl of New Jersey. Clark (1915) did not describe any 'regular' urchins from Delaware, but listed *?Pygurus geometricus* (Morton) and *Cassidulus florealis* (Morton) from the Matawan Formation (Campanian). 'Regular' echinoids from the Upper Cretaceous of Delaware or nearby locations were not recorded by either author.

In the classification used in the *Treatise* (Fell 1966: U408) the genus *Boletechinus* was placed under the heading 'Family Uncertain'. With the addition of other species of *Boletechinus* it becomes clear that the genus shares a number of characters in common with *Zeuglopleurus*, until now regarded as a member of the family Temnopleuridae. In both genera the ocular plates I and V are inset and the compounding of the ambulacral plates follows the acrosaleniid pattern (*sensu* Jensen 1981: 50–55; see Fig. 1.)

In redescribing the American type species of *Boletechinus* and describing the new American species for the first time, it became apparent that close comparison with *Zeuglopleurus* was necessary.

In 1889 Gregory described *Zeuglopleurus costulatus* using specimens E4365, 75556a and 75556b. He regarded 75556a and 75556b as juveniles of the species, but selected no type. In 1900, Gregory described *Z. rowei* using E39372, and also 75556a and 75556b which he no longer regarded as juveniles of *Z. costulatus*. Again, he did not select a type. In the present paper, *Z. rowei* is transferred to the genus *Boletechinus* and *B. rowei* is divided into two subspecies—*B. rowei rowei* and *B. rowei anglicus*. The lectotype of *B. r. rowei* here selected (see p. 76) is one of Gregory's three syntypes—E39372, whilst the holotype of *B. r. anglicus* another of his syntypes—75556a. Gregory's third syntype of *Z. rowei*—75556b—is regarded as a paratype of *B. r. anglicus*. Some additional specimens of *Z. costulatus*, *B. r. rowei* and *B. r. anglicus* are now known.

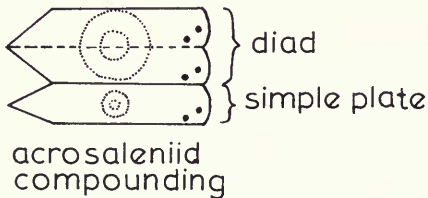


Figure 1a

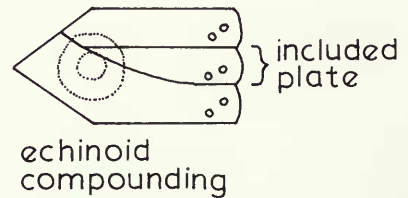


Figure 1b

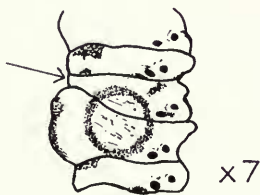


Figure 1c

Zeuglopleurus costulatus showing acrosaleniid compounding

Fig. 1 (a) Diagram to illustrate acrosaleniid compounding. (b) Diagram to illustrate echinoid compounding. (c) Camera lucida drawing to show the kind of acrosaleniid compounding present in an ambulacral plate of *Zeuglopleurus costulatus* (E79244). v indicates component plate having very narrow contact with periradial suture.

The diagnostic characters of the Glyphocyphidae and the Temnopleuridae show that *Zeuglopleurus* and *Boletechinus* belong to neither of these families, and they are therefore placed in the new family Zeuglopleuridae. This should be seen as a plesion within the stem group of the group (Temnopleuridae + Echinoida).

KEY: GSATC = Geological Survey of Alabama, Type Collections.
 USNM, USGS = United States National Museum.
 BM(NH) = British Museum (Natural History). The prefix to registered numbers is E, except for specimens in very old collections.
 GSM = Geological Survey Museum (now British Geological Survey).

Systematic descriptions

Superorder ECHINACEA Claus, 1876

Order TEMNOPLEUROIDA Mortensen, 1942

Family ZEUGLOPLEURIDAE nov.

TYPE GENUS. *Zeuglopleurus* Gregory 1889: 494–495.

DIAGNOSIS. Tubercles imperforate, crenulate; test sculptured along plate margins and around secondary tubercles; ambulacra compounded in the acrosaleniid manner; ocular plates I and V insert; periproct elongate, with large suranal plate(s) included in the disc; gill slits shallow. Family currently includes *Zeuglopleurus*, *Boletechinus*, *Glyptocyphus*, and probably *Echinocyphus*.

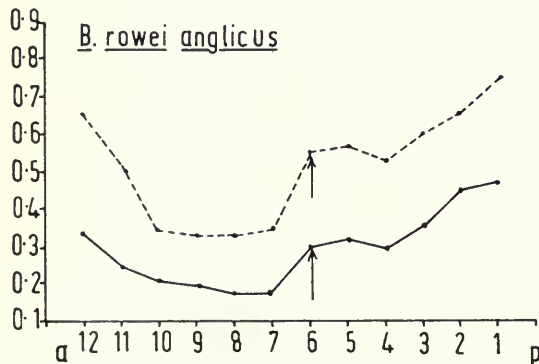
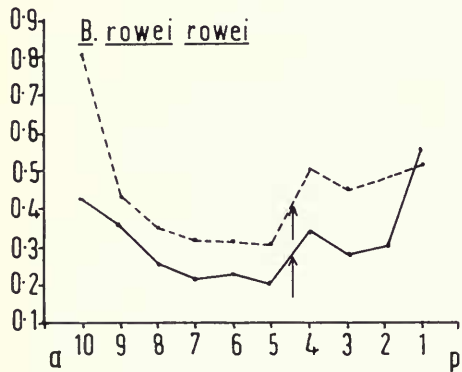
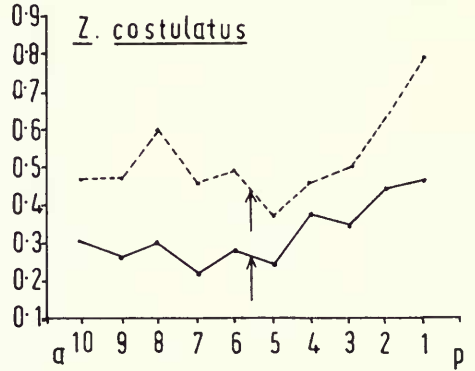
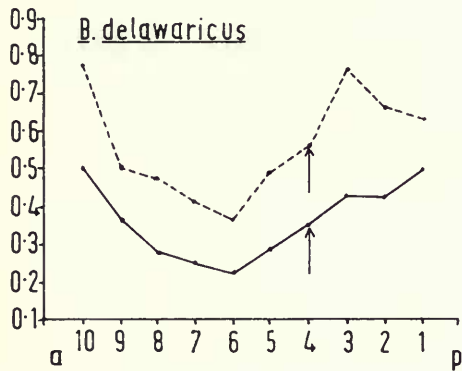
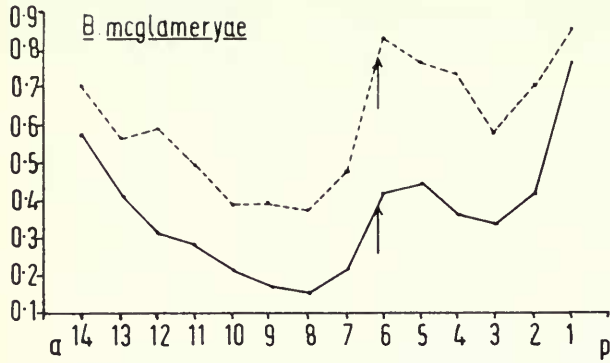
RANGE. Upper Cretaceous of Europe and North America.

DISCUSSION (Figs 2a, 3, 12). Cooke in his diagnosis of *Boletechinus* (1955: 93) was uncertain of its taxonomic position, but he excluded it from the Phymosomatidae because *Orthocyphus*, to which *Boletechinus* bore a resemblance, was dicyclic. He noted also the similarity between *Boletechinus* and '... some of the primitive Arbaciidae ...', the genera having '... large basal tubercles ...'. However, the arbacioids have non-crenulate tubercles and different plate compounding (see Jensen 1981: 55). Cooke's third suggestion was that the genus belonged to the Temnopleuridae as it had a '... coarse surface and indented sutures ...'.

Mortensen (1943: 64) said that, assuming the description and figures by Gregory were representative, *Zeuglopleurus* was an aberrant glyphocyphid because it had the glyphocyphid characters of an 'elongate apical system ...', and '... apparent diadematoïd ambulacral structure ...', but that it was aberrant in having imperforate tubercles. Observations herein of the holotype of *Zeuglopleurus costulatus* show acrosaleniid compounding, verging towards echinoid style compounding, and not the echinoid compounding implied by its inclusion with the Temnopleuridae in the *Treatise* (Fell 1966: U426), and by Mortensen (1943: 67). Mortensen also examined *Z. colleti* by grinding down part of an ambulacrum and concluded that the compounding is echinoid. If this is the case, then *Z. colleti* is not a *Zeuglopleurus* but a temnopleurid as defined in the *Treatise*.

In an attempt to place *Zeuglopleurus* and *Boletechinus* in their correct taxonomic position it is necessary to consider the Glyphocyphidae and Temnopleuridae (see Fig. 12, cladogram, p. 87).

Most glyphocyphids are classified in the *Treatise* as having characters which include acrosaleniid plate compounding, apical disc either monocyclic or with ocular plates I and V insert, and perforate tubercles. The *Treatise* also includes in the glyphocyphids genera which do not have all the glyphocyphid characters; examples are *Echinopsis* which has echinoid compounding, and *Progonechinus* which has echinoid compounding and apparently non-crenulate, imperforate tubercles (but this appearance is questioned by Mortensen as being caused by the preservation of the fossil).



KEY

horizontal axis:-
number of interamb. plate

vertical axis:-
1. length of primary tubercle /
length of plate: ———
2. length of primary tubercle /
height of plate: - - - -

a :- apical disc

p :- peristome

↑ :- ambitus

Figure 2a

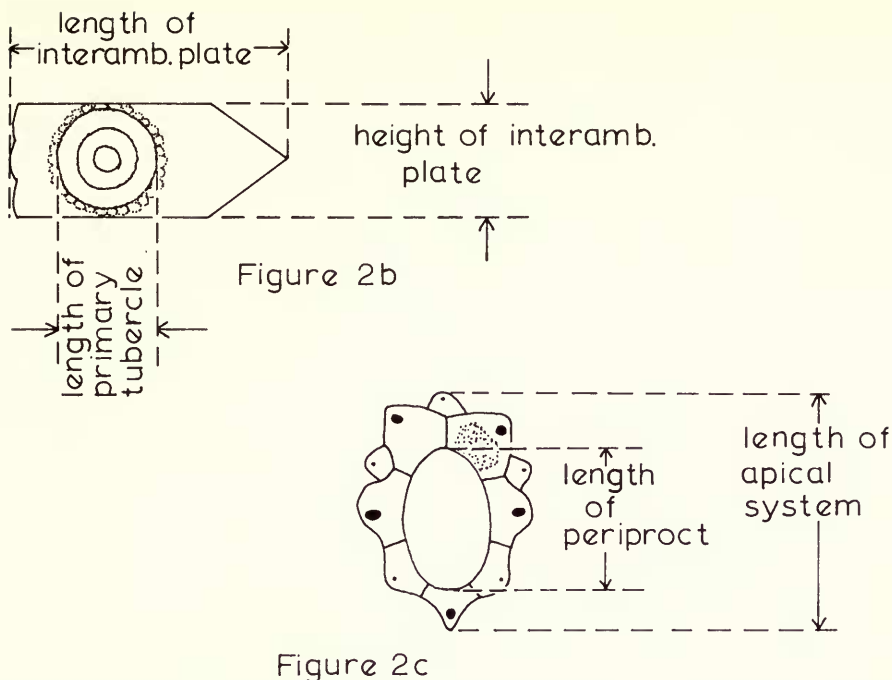


Fig. 2 (a) Graphs to show the abrupt increase in the size of the primary tubercles at the ambitus for the holotype of each species, with the following data plotted:

$\frac{\text{length of primary tubercle}}{\text{length of interambulacral plate}}$ plotted against the number of the plate, and

$\frac{\text{length of primary tubercle}}{\text{height of interambulacral plate}}$ plotted against the number of the plate.

(b) Diagram to illustrate the measurements of an interambulacral plate.

(c) Diagram to illustrate the measurements of the apical disc.

The characters which currently unite the temnopleurids as classified in the *Treatise* include imperforate tubercles and echinoid plate compounding. Most temnopleurids have dicyclic apical discs, but some have one or more ocular plates insert. The compounding of the ambulacral plates is generally held to be of echinoid type, but illustrations of compounding given by Mortensen and others suggest that this may not always be the case, and that diadematoïd or acrosaleniid compounding may occur, for example as in *Paratrema* (Mortensen 1943: 45, fig. 42b), *Hypsiechinus* (1943: 45, fig. 42a), and *Lamprechinus* (1943: 337, figs 195a, b). Further research is needed to check this.

The most characteristic features to distinguish the family Zeuglopleuridae are: ocular plates I and V insert; tessellation into the apical disc of one or more large suranal plates. In other respects the family resembles some of the more primitive members of the Temnopleuridae in that it has imperforate tubercles and prominent sculpturing of the test, but not properly developed echinoid plate compounding. So far, three or four genera have been recognized as belonging to the Zeuglopleuridae—*Zeuglopleurus*, *Boletechinus*, *Glyptocyphus*, and probably *Echinocyphus*. According to A. B. Smith (personal communication, and in preparation) the type species of *Glyptocyphus*, *G. difficilis*, has ocular plates I and V insert and large suranal plates included in the apical disc. It has a sculptured test, and plate compounding which is acrosaleniid but which is irregular in its development, even in the same specimen. All these characters

justify including the genus in the new family. The type species of *Echinocyphus*, *E. tenuistriatus*, has a sculptured test, and plate compounding which is acrosaleniid and regularly developed. The apical disc is unknown, but if it should prove to have ocular plates I and V insert, the genus will probably belong to the Zeuglopleuridae. Revision of the Temnopleuridae as defined in the *Treatise* may reveal more members of the Zeuglopleuridae.

The synapomorphies of *Zeuglopleurus* and *Boletechinus* are those of the Zeuglopleuridae, but the abrupt increase in the size of the primary tubercles at the ambitus of *Boletechinus* differs from the steady increase in size of the primary tubercles of *Zeuglopleurus*.

The difference between acrosaleniid compounding and echinoid compounding can be very slight and may depend on whether there is a demiplate present or not. In the case of acrosaleniid compounding all components of a compound plate touch the perradial suture, whereas an echinoid compound plate has one or more demiplates present. In *Zeuglopleurus* (for example, E79244, Fig. 1c) the area of contact with the perradial suture by one component plate is very narrow indeed. It seems likely that close examination of the compounding of some temnopleurids will also show a similar narrow contact with the perradial suture.

Although most temnopleurids have many periproctal plates, some have a few large periproctal plates which are incorporated into the structure of the apical disc. A single large plate was present in *Boletechinus* (see Fig. 10, p. 79) and, although none are preserved, one or more large plates were probably present in *Zeuglopleurus* as is suggested by the angular, elongated periproct with facets for the attachments of periproctal plates (see Fig. 11d, p. 83). Acrosaleniids, as well as having acrosaleniid plate compounding, have large suranal plates tessellated into the apical disc, suggesting the possibility that the Selenioida form the sister group of the Zeuglopleuridae.

It is also interesting to note that where there appears to be acrosaleniid compounding in members of the Temnopleuridae the periproctal plates are reduced in number and increased in size, but where the compounding is certainly echinoid, the periproctal plates are more numerous and much smaller (see text-figures by Mortensen, 1943).

To summarize, with reference to the cladogram (Fig. 12, p. 87), the Glyphocyphidae and the Zeuglopleuridae are both plesions within the stem group of the Temnopleuridae + Echinoida (= Camarodonta *sensu* Jackson 1912: 183).

CONCLUSION. The Zeuglopleuridae, at present comprising *Zeuglopleurus*, *Boletechinus*, *Glyptocyphus*, and probably *Echinocyphus*, form a plesion in the stem group of Temnopleuridae + Echinoida. The autapomorphies of the new family include: ocular plates I and V insert; elongate periproct with large suranal plate(s).

Zeuglopleurus is readily distinguished from *Boletechinus* by the abrupt increase in size of the primary tubercles at the ambitus of *Boletechinus*. Further research is necessary to determine whether any other genera of the Temnopleuridae should be included in the Zeuglopleuridae, and examination of the Glyphocyphidae and Temnopleuridae may show that there are more natural groupings than just three.

Genus *BOLETECHINUS* Cooke 1955

TYPE SPECIES. *Boletechinus mcglameryae* Cooke 1955.

DESCRIPTION. *Shape:* A small zeuglopleurid with a hemispherical test, slightly higher at the anterior end than at the posterior end.

Apical System: 1) Ocular plates. Ocular plates I and V are insert and are between 15% and 25% larger than oculars II, III, and IV. There is an elongated M-shaped margin next to ambulacra I and V and an ocular pore just adoral to the centre of the M. Oculars II, III, and IV have less elongate M-shaped margins next to ambulacra II, III and IV, with the ocular pore just adoral to the centre of the M. All the ocular pores are perradial in position. The ornament consists of several small tubercles.

2) Genital plates and madreporite. These form the anterior, lateral, and posterior-most margins of the periproct. Genital plate 5 is the smallest and has the shape of a short stubby

boomerang, has an interradial pore, and a slight swelling of the adoral margin into the periproct. The genital pores of plates 1, 3 and 4, and of plate 2 when recognizable, are very slightly anteriorly adradial in position. The madreporic part of plate 2 is a prominent swelling and is perforated by many tiny pores. The ornament of genital plates 1-4 consists of tubercles or pits, whilst plate 5 lacks any large ornament.

3) Periproct. This is elongated along the anteroposterior axis. The longer dimension is usually between 15% and 25% greater than the shorter. The rim of the periproct formed by oculars I and V and genital plates 1-4 is either raised or level with the surface of the test, whilst the rim formed by genital plate 5 is level with the surface of the test or very slightly lower.

Ambulacra: These are straight, taper adapically and adorally and are widest at the ambitus. There are between about 4 and 12 simple plates, counting from the apical disc adorally, and then up to about 9 compound plates to the peristome. The plates are compounded in the acrosaleniid manner. The pore pairs are in monoserial columns, and are similar, and oblique so that the adradial pore is more adapical than the perradial pore. The pores of a pair are separated by a thin wall, and the pair is surrounded by a low wall, with a gap at the perradial adoral margin. The ornament of the ambulacra consists of primary and secondary tubercles and sculpturing or excavation of the test.

The primary tubercles each consist of a low, convex, circular boss, a parapet with 10 to 14 crenulations, a short neck and an undercut, imperforate, hemispherical mamelon. If a column is followed from the apical disc adorally, the size of the primary tubercles is seen to increase abruptly near the ambitus.

Secondary tubercles have low convex bosses with small mamelons. The tubercles vary in size and give a granular appearance to the ambulacra.

Sculpturing of the ambulacra occurs along plate margins and around the tubercles, sometimes giving a rough appearance to the test.

Interambulacra: These taper adorally and adapically and are widest at the ambitus. The ornament consists of primary and secondary tubercles and sculpturing or excavation of the test. There are up to 14 plates per interambulacrum in each column.

The primary tubercles and the secondary tubercles of the interambulacra have a similar structure to those of the ambulacra, with up to 14 crenulations on the primary tubercles. If a column is followed adorally from the apical disc, the size of the primary tubercles is seen to increase abruptly near the ambitus. The sculpturing occurs along plate margins and around the tubercles, sometimes giving a rough appearance to the test.

Peristome: This is decagonal and has shallow gill slits.

RANGE. Upper Cretaceous of Europe and North America.

REMARKS. The abrupt increase in the size of the primary tubercles at the ambitus of *Boletechinus* readily distinguishes the genus from *Zeuglopleurus*, whose tubercles increase in size gradually (Figs 2a, b, 3a-f).

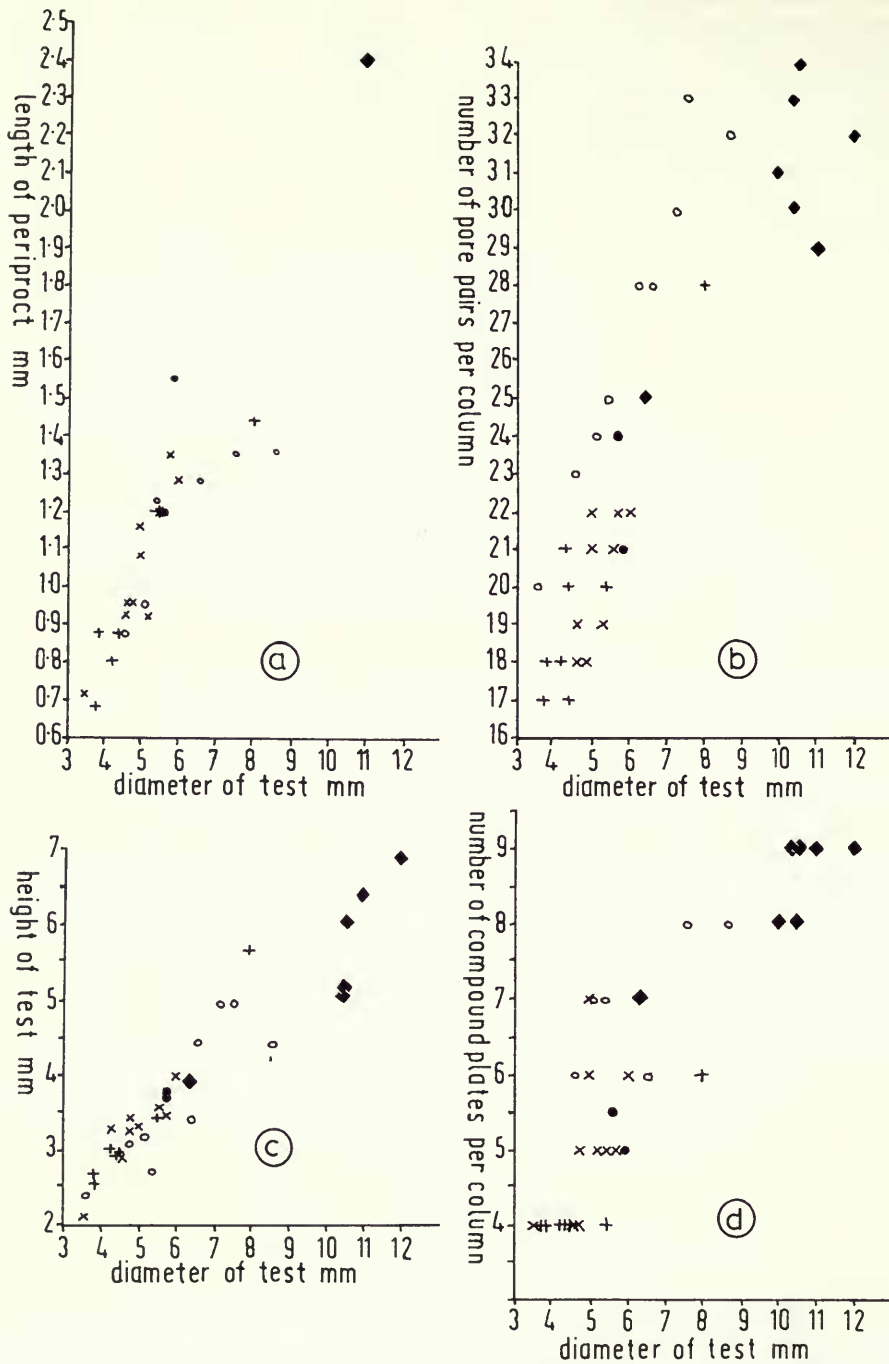
Boletechinus mcglameryae Cooke

Figs 2a, 3a-f, 4a-f

1955 *Boletechinus mcglameryae* Cooke: 93; pl. 28, figs 11-16; text-fig. 4.

DIAGNOSIS. A *Boletechinus* whose test from ambitus adapically has a very granular appearance, with secondary tubercles close together over the surface of each plate. Plate boundaries not very distinct, partly obscured by ornament. Two thin, almost parallel ridges form inverted V on adoral sides of plates, prominent above ambitus, less distinct adorally. Primary tubercles from ambitus to oral surface relatively small. Periproct angular, slightly elongated.

MATERIAL. Holotype: GSATC 108, from the Cretaceous, Maastrichtian, Prairie Bluff Chalk; from 2 miles north of Livingstone, Sumter County, Alabama (Figs 4a-f).



KEY: o *B. mcglameryae*; ● *B. delawaricus*; ◆ *Z. costulatus*;
 x *B. rowei rowei*; + *B. rowei anglicus*.

Figure 3

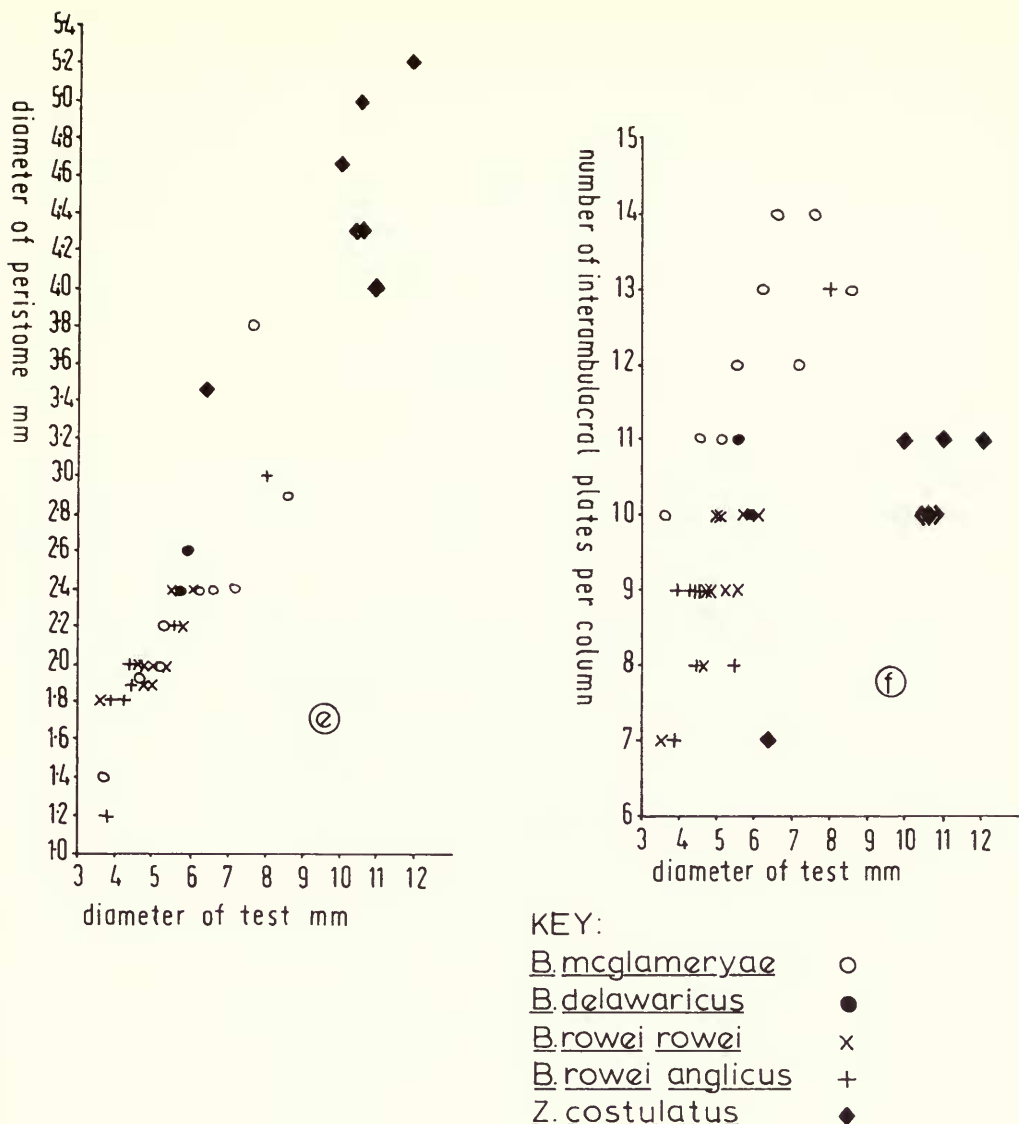


Figure 3

Fig. 3 (a) Graph to show the close similarity between species of *Boletechinus* when the length of the periproct is compared with the diameter of the test. *Zeuglopleurus costulatus* (holotype) falls outside the *Boletechinus* cluster. (b) Graph compares the diameter of the test with the number of pore-pairs per column for each species. *Z. costulatus* falls outside the *Boletechinus* cluster. (c) Graph compares the diameter of the test with its height for each species. *Z. costulatus* is separated from the *Boletechinus* cluster. (d) Graph compares the diameter of the test with the number of compound plates per column for each species. *Z. costulatus* is separated from the *Boletechinus* cluster. (e) Graph compares the diameter of the test with the diameter of the peristome for each species. *Z. costulatus* falls far outside the *Boletechinus* cluster. (f) Graph compares the number of interambulacral plates with the diameter of the test for each species. *Z. costulatus* is separated from the *Boletechinus* cluster. N.B. All the graphs illustrate the difficulty of separating the species by comparing measurements and numbers of components of the test.

Paratypes: GSATC 108 from the same locality; USNM 108689 (figured by Cooke 1955: pl. 28, figs 14–16) and USGS 18636 from the same locality.

SHAPE. The test is hemispherical, slightly lower at the posterior end. Some specimens are flattened so that the test is almost discoidal. Dimensions of the holotype (mm): diameter of test 7.6, height of test 4.9, diameter of peristome 2.8.

PRESERVATION. The holotype is uncrushed, slightly abraded and is filled with a pinkish grey matrix. The GSATC paratypes are filled with a cream-coloured matrix, and are less abraded. The apical disc of one specimen has been pathologically displaced towards ambulacrum I and interambulacrum 1, thereby elongating the adapical ambulacra and interambulacra of the opposite side, and shortening those on the same side. There is also a slight indentation of the test at interradius 5 in this specimen. The USNM specimen figured by Cooke (1955) is uncrushed, slightly abraded, and a small part of interambulacrum 3 adoral to the ambitus is missing. The specimen is filled with a cream-coloured matrix. The other USNM specimens are undamaged and have a pale grey matrix.

APICAL SYSTEM (Fig. 4f). 1) Ocular plates. Ocular plates I and V are about 25% longer than oculars II–IV. The outline of oculars I and V is approximately hexagonal, with a very broad V-shaped periproctal margin. The M-shaped margin has small pits on the surface. Oculars II–IV each have a rounded M-shaped margin, and have an ocular pore situated near the adoral periradial margin of each plate.

Ornament consists of three or more tubercles on each plate; on oculars I and V they are present along the periproctal edge of the plate; on oculars II–IV they are grouped together at the periproctal end. There are also many small pits present on the non-tubercular parts of the oculars.

2) Genital plates and madreporite. The periproctal margins are each gently concave. Plates 1 and 4 are elongated at their anterior ends, and have five other sides. The madreporite is formed on the anterior two-thirds of genital plate 2. Genital plate 3 has the same outline shape as genital plate 2, but is about three-quarters of the size. The posterior-most part of the periproct formed by genital plate 5 has an outline of a very elongate and angular U, so that this margin and the adjacent margins of oculars I and V appear scalloped. The genital pores of plates 1, 3 and 4 are quite large and slightly oval, and with the long axis interradiial. Genital plate 5 has a circular pore near the adoral margin.

The ornament of genital plates 1–4 consists of a few small tubercles and fairly deep pits. Genital plate 5 has no ornament. There is a single pit between genital plates 1 and 2, 2 and 3, and 3 and 4. There is no pit between genital plate 5 and oculars I and V. The elongated appearance of genital plate 5 is due to its two long margins being straighter than the equivalent, convex, margins of the other genital plates. These two straight sides meet at a sharper angle than do their equivalents in the other genital plates. The dimensions of genital plates in the holotype are given in Table 1.

Table 1 Dimensions of genital plates in holotype of *Boletechinus mcglameryae* Cooke. L = maximum length between adradial margins; W = maximum width, periproctal margin to interradius (mm).

Plate	L	W
1	0.76	0.6
2	0.9	0.66
3	0.7	0.64
4	0.72	0.6
5	0.66	0.4

3) Periproct. This has an angular outline, with straight margins at oculars I and V and genital plates 1-4. Genital plate 5 has a V-shaped periproctal margin. The periproct is also elongated along the anteroposterior axis. The paratype figured by Cooke (1955) has a smoother, slightly greater than semicircular outline in the anterior part, and a scalloped outline in the posterior part. The longer dimension is about 20% greater than the shorter in Cooke's figured paratype and about 40% in the holotype. The margin of the periproct is level with the surface of the test, except at genital plate 5 where it is slightly concave.

AMBULACRA (Fig. 4d). The ratios of the width of the ambulacra to the width of the interambulacra of the holotype are:

at the apical disc	1 : 2
at the ambitus	1 : 1.8
at the peristome	1 : 1.5

The pores are circular, similar, and surrounded by a flat rim whose adoral perradial side is partly obscured by the adoral adradial margin of the next adoral plate. The plates are simple from the apical disc to a position just adapical to the ambitus. The succeeding plates are acrosaleniid compounds.

Smaller primary tubercles are present from the apical disc to the ambitus, whilst larger primary tubercles, with about 12 crenulations, occur abruptly at the ambitus together with an abrupt increase in the diameter of the scrobicules. Adorally, the decrease in size is gradual. The secondary tubercles of smaller simple plates are present on the perradial ends of the plates and are approximately the same size as the primary tubercles, whilst on larger simple plates there are two or three secondary tubercles in this position. Adoral to the primary tubercle of the simple plate there is a single tubercle connected to the boss by a small ridge. On the compound plates there are two secondary tubercles and two ridges forming an inverted V-shape on the adoral side of the compound plate. The adoral ends of the ridge join two secondary tubercles on the simple plate between adjacent compound plates. At the ambitus and adorally, the ridges become much less distinct. This arrangement produces a weak, discontinuous rib extending from the apical disc to the larger primary tubercles at the ambitus.

The compound plates with large primary tubercles each have secondary tubercles along the adapical margins and the perradial margins, and the simple plate has a row of secondary tubercles plus a small primary tubercle. Together, a horseshoe-shape of secondary tubercles is formed but without a distinct continuation of the ribs formed adapically.

Sculpturing between adjacent secondary tubercles gives the ambulacra a coarse appearance. The adapical margins of the simple plates on the adapical part of the ambulacra are raised, giving the plates a tilted appearance.

There are between about 5 and 12 simple plates and between about 5 and 9 compound plates to each ambulacral column for tests with diameters between 3.7 mm and 8.7 mm.

INTERAMBULACRA (Fig. 4e). These broaden rather rapidly from the apical disc to the ambitus, then taper gently to the peristome. The adapical margins of the plates are raised slightly above the general surface of the test to give a tilted appearance to the plates.

Each primary tubercle has about 14 crenulations. Secondary tubercles are present as incomplete scrobicular circles on each plate. They are situated along the adradial and interrarial margins of the plate, with 4-6 of them along each margin. The secondary tubercles are all about the same size as a small primary tubercle of an ambulacrum. Further secondary tubercles of this size are present along the plate margins.

Between the adoral side of the boss of the primary tubercle and the adapical side of its adoral neighbour there are thin rounded ridges, which form an inverted V-shape with almost parallel sides. The adoral ends of the V are two small secondary tubercles on the adjacent adoral plate. Sometimes a third ridge is present, either adradial or interrarial in position. The ridges plus primary tubercles produce on each interambulacrum an appearance of two discontinuous ribs extending from the apical disc to ambitus. At the ambitus the V-shape opens out and the ridges

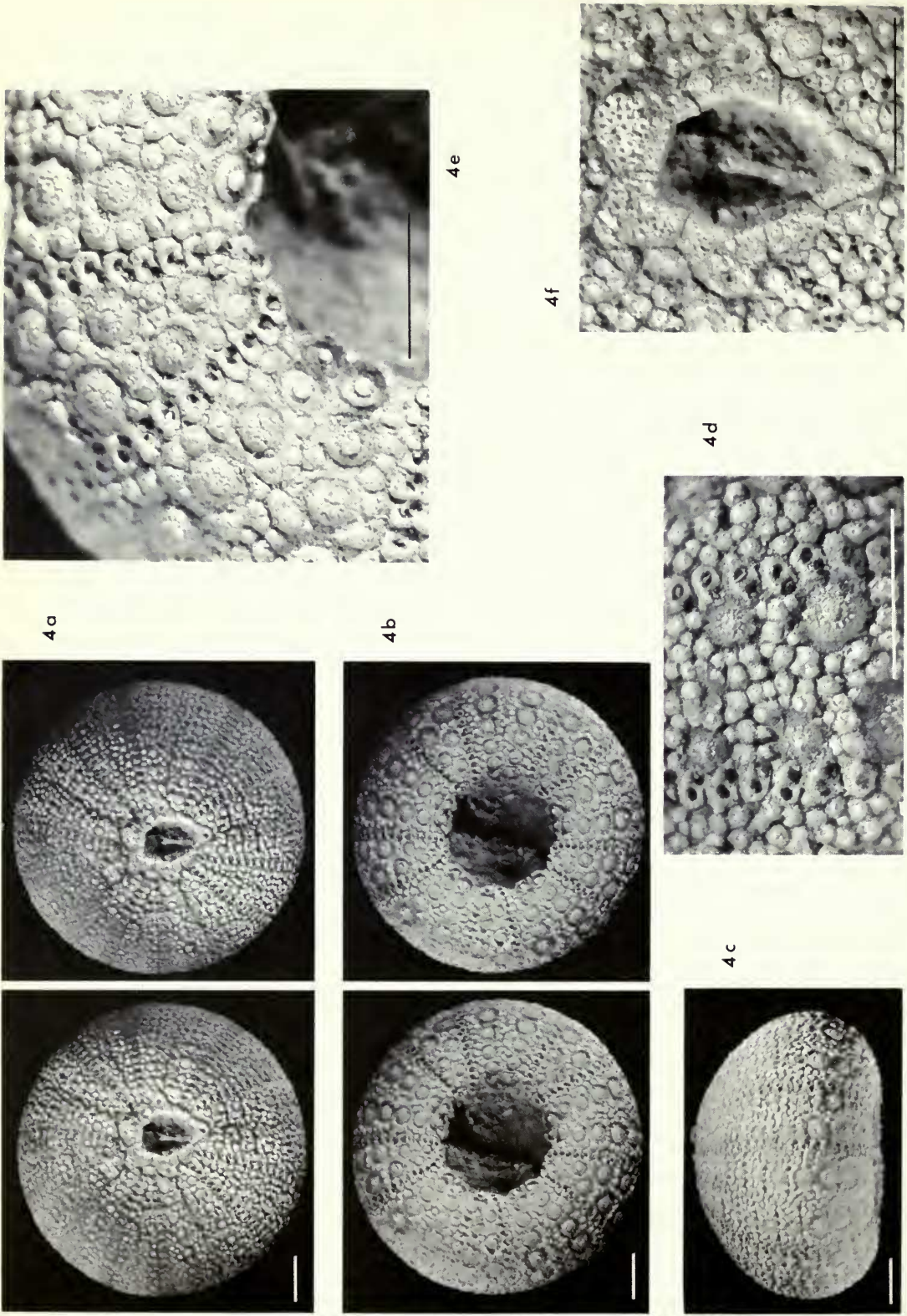


Fig. 4 *Boletechinus meglameryae* Cooke, holotype GSA TC 108. (a), stereo photograph of apical view; (b), stereo photograph of oral view; (c), side view; (d), close-up of ambulacral ornament; (e), detail of part of the peristome; (f), apical disc. Scale bars 1 mm.

become much reduced in size. The plates are excavated around each secondary tubercle and between the ridges, to give a rough texture to the test.

There are 10–14 plates to each interambulacral column for tests with diameters between 3.7 mm and 8.7 mm.

PERISTOME (Figs 4b, 4e). The diameter of the peristome is about 37% of the diameter of the test, with some primary and secondary tubercles protruding into the peristome.

Boletechinus delawaricus sp. nov.

Figs 2a, 3a–f, 5a–d, 6, 7

DIAGNOSIS. A *Boletechinus* with diamond-shaped depression between adoral edge of one interambulacral primary boss and adapical edge of adjacent interambulacral boss. Depression bordered by divergent adradial and interrarial ridges which may enclose an additional ridge consisting of components of both constituent plates. Test with well-defined plate boundaries. Primary tubercles at ambitus and on oral surface relatively large. Periproct oval.

MATERIAL. Three specimens from the Upper Cretaceous, Monmouth Group, Navesink Marl (= Maastrichtian; see Spangler & Peterson 1950: 8), from the Delaware Canal, Delaware, U.S.A., were given by Mr Allan Graffham, owner manager of 'Geological Enterprises' in Oklahoma, to Mr R. Baker who presented them to the British Museum (Natural History) in 1979.

TYPES. Holotype: E76803 (Fig. 5); Paratypes: E76804 (Fig. 7), E76805 (Fig. 6).

PRESERVATION. Two of the specimens are uncrushed but have been slightly abraded. Paratype E76805 has the remains of a membraniporid bryozoan attached to the test.

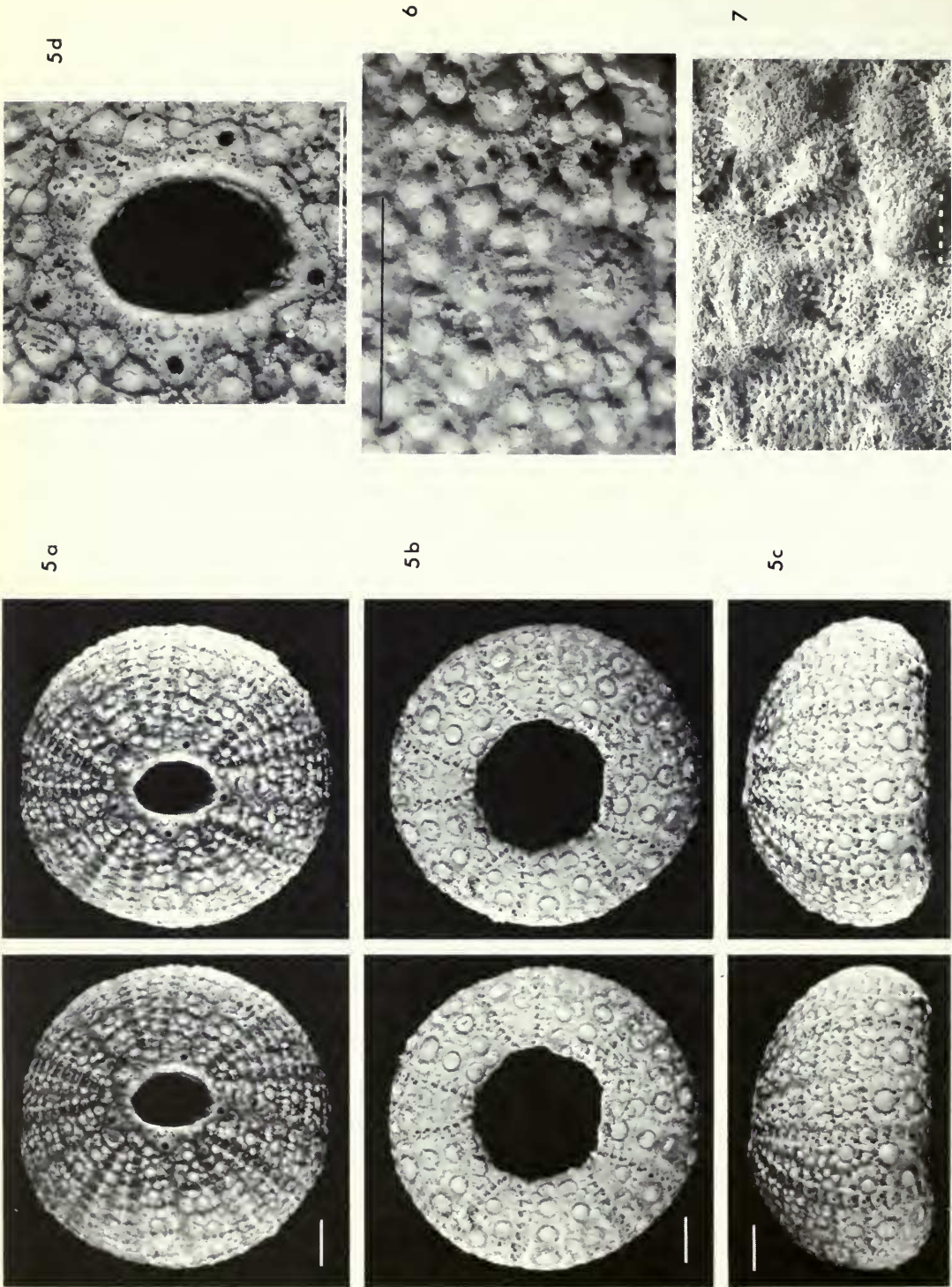
SHAPE. The specimens are approximately hemispherical, with the anterior end slightly higher than the posterior end. There is a circular peristome of moderate size and an elongate periproct with a slightly raised margin.

Table 2 Dimensions (mm) of holotype and paratypes of *Boletechinus delawaricus* sp. nov.

	Diameter	Height	Diameter of peristome
Holotype E76803	5.9	3.7	2.6
Paratype E76804	5.9	3.6	2.3
Paratype E76805	5.7	3.7	2.4

APICAL SYSTEM (Fig. 5d). 1) Ocular plates. Ocular plates I and V are 15–20% longer than ocular plates II, III and IV. The outline of oculars I and V is approximately hexagonal, with a gently concave periproctal margin. The M-shaped margin at ambulacra I and V is flattened. Oculars II, III and IV are approximately pentagonal, and have flattened M-shaped margins. The ornament of each plate consists of a large tubercle adapical to the pore and a few smaller tubercles or granules next to the large tubercles. The details of the ornament of the tubercles have been removed by abrasion. At all the margins except the M-shaped ones there are fine striations perpendicular to the sutures. These striations pass from the base of the tubercles to the margins of the plates, are continuous with those of adjacent genital plates, and run indistinctly onto adjacent interambulacral plates.

2) Genital plates and madreporite. The periproctal margin of each genital plate is strongly concave. Genital plates 1 and 4 are more elongated at their anterior ends, and each has six sides. The elongation of genital plates 1 and 4 makes them asymmetrical in outline, unlike the bilaterally symmetrical outlines of plates 2 and 3. Genital plates 2 and 3 have seven sides. The



Figs 5-7 *Boletechinus delawarensis* sp. nov. Fig. 5, holotype E76803. (a), stereo photograph of apical view; (b), stereo photograph of oral view; (c), stereo photograph of side view; (d), apical disc. Fig. 6, paratype E76805. Interambulacral ornament, showing abrupt increase in tubercle size, and the additional ridge in the diamond-shaped depression between adjacent plates. Fig. 7, paratype E76804. S.E.M. photograph to show the diamond-shaped depression between adjacent interambulacral plates. Scale bars 1 mm (Fig. 7, 0.1 mm).

ornament of genital plates 1, 3 and 4 consists of a single large tubercle close to the middle of the periproctal margins, and several well-defined, small, shallow pits are present near the plate margins bordering ocular plates II, III and IV. Also present are fine striations, perpendicular to these same margins, and continuous with the striations of adjacent ocular plates.

Each genital pore is large, and fairly close to the edge of the plate. The madreporic part of genital plate 2 is perforated with many holes a little less in diameter than the genital pores. The ornament of genital plate 2 consists of the fine striations, as present in genital plates 1 and 4, but there are fewer shallow pits. There is a single large tubercle which has become partly incorporated into the raised madreporic part of the plate.

Genital plate 5 has an interradiial genital pore equidistant from the posterior margins and the periproctal margin. There is no conspicuous ornament. The periproctal margins of the genital and ocular plates have rounded edges.

Table 3 Dimensions of genital plates in holotype of *Boletechinus delawaricus* sp. nov. L = maximum length between adradial margins; W = maximum width, periproctal margin to interradiial suture (mm).

Plate	L	W
1	0.7	0.4
2	0.7	0.6
3	0.8	0.6
4	0.75	0.5
5	0.7	0.3

3) Periproct. This has the outline of an elongated pentagon with curved sides. The longer dimension, along the anteroposterior axis, is about 25% greater than the shorter dimension from genital plate 1 to genital plate 4. The margin of ocular and genital plates is slightly raised except at genital plate 5 which is level with the surface of the test.

AMBULACRA (Fig. 6). The ratios of the width of the ambulacra to the width of the interambulacra of the holotype are:

at the apical disc 1 : 2.5
 at the ambitus 1 : 1.4
 at the peristome 1 : 1.7

The adapical sides of the plates are raised slightly to give a tilted appearance. The first 4 to 12 plates from the apical disc adorally are simple, then 3 to 5 acrosaleniid compound plates continue to the peristome.

The pore-pairs of each plate—both simple and compound—are situated on an area whose outline is approximately square. They are oblique, circular, similar, and each pair is separated from its neighbour by a thin wall. The perradial pore is open at its adoral margin.

Larger primary tubercles are low, with between about 10 and 14 coarse crenulations. The tubercle is central in position on each compound plate and covers most of it. Smaller primary tubercles are situated on the centre of each of the simple plates adapical to the ambitus. On the first few compound plates the adapical quarter or third of the boss overlaps the adoral margin of the adjacent adapical plate and together with adoral and adapical secondary tubercles, and the primary tubercle of simple plates, form interrupted ridges adapical to the ambitus. Single secondary tubercles occur on the perradial margins of the simple plates, several secondary tubercles occur along the perradial margins of the compound plates—usually two on the adapical and two on the adoral perradial margins—and three secondary tubercles are present on the simple plates between compound plates.

Broad grooves extend from between each secondary tubercle to the boss of the primary tubercle. The sutures between the simple plates of the ambulacra adapical to the ambitus are well defined, whilst those between the compound plates and simple plates are less well defined. The definition is enhanced by the slight excavation along the margins of each plate, and between each simple plate and each compound plate adjacent to a simple plate there is a triangular pit on the adapical margin. The apex of the triangle is adoral, the base extends from the adradial margin of the plate to the perradial part of the 'square' containing the pore-pairs.

INTERAMBULACRA (Figs 6, 7). The adapical margins of the plates are slightly raised to give a tilted appearance to each plate. The larger primary tubercles have between 11 and 14 coarse crenulations. The secondary tubercles form scrobicular arcs, and appear as small hemispheres about the same size as the mamelon of a primary tubercle, and are close together. There are usually three of them along each adradial and interradian margin, and some near the adradial adapical edges of the plates. Between adjacent secondary tubercles is a very shallow depression extending to the base of the primary boss, giving the scrobicule a slightly crenulated appearance. On the adapical and adoral sides of each plate there are two ridges which radiate from the base of the boss and meet the ridges of the adjacent plates adorally and adapically. The ridges enclose a small diamond-shaped depression (Fig. 7). In paratype E76805 additional ridges are frequently included within the diamond shape and are continuous from the adapical to the adjacent adoral plate, and occur from the ambitus adorally (Fig. 6). Seen from a distance, the ridges and primary tubercles give the appearance of two discontinuous ribs along the interambulacral columns, less well defined on the oral surface.

The sutures between each plate are well defined and are very slightly excavated. The interradial suture is also excavated and tapers very gradually to the oral surface, close to the peristome. There are about 10 or 11 plates in an interambulacral column, with a test diameter of between 5.7 mm and 5.9 mm.

PERISTOME (Fig. 5b). The diameter is about 43% of the diameter of the test, and the outline is pentagonal with rounded angles. The five straight sides are interambulacral and the rounded angles are ambulacral. The holotype has all the apophyses preserved and auricle IVb, but the other auricles have been broken off at their bases. The auricle is a U-shaped structure which is tilted upwards away from the peristome. It is short and has rounded tips, and shows the retractor-muscle scars. The apophyses form lower, convex swellings with distinct sutures at their adradial margins with the auricles. The perignathic girdle of the paratype E76805 is obscured by matrix.

Boletechinus rowei (Gregory)

1900 *Zeuglopleurus rowei* Gregory: 353–354, figs 1–4.

1943 *Zeuglopleurus rowei* Gregory; Mortensen: 352–353.

DIAGNOSIS. A *Boletechinus* with very oblique pore-pairs. Two ridges composed of coalesced secondary tubercles on adoral side of plates extend from primary boss to adoral scrobicular tubercles. Primary tubercles from ambitus to oral surface relatively small. Periproct slightly elongated.

There are two sub-species, *B. rowei rowei* and *B. rowei anglicus* subsp. nov.

SHAPE. The shape is circular, or a rounded pentagon; approximately hemispherical, with the anterior end slightly higher than the posterior end. Periproct is slightly elongated; peristome is decagonal.

APICAL DISC. 1) Ocular plates. Oculars I and V are about 25% longer than oculars II–IV. The periproctal margins of oculars I and V are concave, slightly angular. The outline of oculars I–V is angular, with plates II–IV approximately pentagonal. The ornament varies between the subspecies. The shape of the apical disc is slightly ovoid, with the elongation along the antero-posterior axis.

2) Genital plates and madreporite. The non-periproctal margins are straight, and convexly rounded at the interradius. The genital pores are quite large, and are situated in an approximately circular raised area composed of a few coalesced tubercles. Ornament consists of several granular tubercles about the same size as the secondary tubercles elsewhere on the test. Between the tubercles and around the raised circular area containing the genital pore, the test is sculptured to a greater or lesser amount. Genital pore 5 has a slightly raised rim which bulges into the periproct. The periproctal margins of genital plates 1-4 have the outline of a broad, asymmetrical V-shape, the longer side anterior. The periproctal margin of genital plate 5 is a regular V-shape, with a slight bulge into the dip of the V. Along the periproctal margins there are a few quite large tubercles with sculpturing between them. The madreporite is an irregular swelling with many perforations which may obscure the position of the genital pore. When the genital pore of plate 2 is obvious, it is situated on a low, unornamented part of the plate.

3) Periproct. The periproct is slightly elongated anteroposteriorly, and is between 15% and 25% longer than wide. It varies in outline from a slightly elongated circle to an elongated pentagon. At the junction between one marginal plate and its neighbour there is a slight swelling into the periproct, giving it an undulating outline. This is better seen in a periproct with pentagonal outline.

AMBULACRA. The ambulacra are composed of both simple and compound plates. There are between 5 and 10 simple plates and between 3 and 7 compound plates in each column for tests of diameters between 3.8 mm and 8 mm. Simple plates occur from the apical disc adorally, and compound plates from just apical of the ambitus to the peristome. The pores of a pair are similar and very oblique—the adradial pore is almost directly adapical to the perradial pore. They are slightly elongated, almost teardrop-shaped, with the long axis of the adapical pore approximately parallel to the transverse suture, and the long axis of the perradial pore obliquely perradial-adradial. The pores are sunken into the plate and are separated from each other by a low wall or ridge. A rim around each pair of pores is much taller at the adradial edge than diagonally opposite at the perradial edge, and gives an obliquely tilted appearance to that part of the plate, almost to isolate it from the rest of the plate.

The primary tubercles have up to 14 crenulations, depending on the size of tubercle. Secondary tubercles have a granular appearance and are approximately the same size as the mamelon of a large primary tubercle. On the most adapical plates there is one secondary tubercle near the perradial edge of the plate, but elsewhere there are two. Further adorally, on small diad compound plates, secondary tubercles form small clusters around primary tubercles. On larger compound plates, secondary tubercles form adradially incomplete, non-confluent scrobicular circles, separated by the simple plate bearing its own primary and secondary tubercles. On compound plates from the ambitus adorally, the scrobicules may be excavated from the boss to the secondary tubercles to give a spoked effect of radiating ridges. There are also many extrascrobicular tubercles.

INTERAMBULACRA. The width of an interambulacrum is about half as much again as an ambulacrum. The ratio of the width of each interambulacrum at the apical disc, ambitus and peristome is 1 : 2.4 : 1. The primary boss has up to 14 crenulations, depending on size. Secondary tubercles are approximately the same size as the mamelon of a larger primary tubercle, and have a granular appearance. The secondary tubercles form contiguous scrobicular arcs which are approximately semicircular, and are also present elsewhere on the plate as numerous extrascrobicular tubercles, sometimes forming additional though incomplete arcs. The scrobicular tubercles adapical to the ambitus are situated very close to, or are in contact with, the primary boss. At the ambitus, at the abrupt increase in the size of the primary tubercles, and adorally, there is a distinct but narrow scrobicule between the primary base of the primary boss and the scrobicular tubercles, frequently with excavations in the surface from boss to secondary tubercle, forming a spoked appearance to the plate. The prominence of the spoked effect varies with the subspecies. There are between 7 and 13 interambulacral plates per column for tests with diameters of between 3.8 mm and 8 mm.

PERISTOME. The ratio of the width of the ambulacra to the width of the interambulacra at the peristome varies from 1 : 1.2 to 1 : 1.9 (mean 1 : 1.5), depending on size of test. The gill slits have low rims around their edges, and these extend onto the outer surface of the interambulacra. The apophyses are thick ridges; the auricles are short pegs which are not joined, and have distinct retractor-muscle scars.

***Boletechinus rowei rowei* (Gregory)**

Figs 2a, 3a-f, 8a-e

1900 *Zeuglopleurus rowei* Gregory: 353-354, figs 1-3.

1943 *Zeuglopleurus rowei* Gregory; Mortensen: 352.

DIAGNOSIS. A *Boletechinus* whose plate boundaries are obscured by secondary tubercles, which give a granular stellate appearance to the ornament adapical to the ambitus. Stellate ornament not present from ambitus adorally.

LECTOTYPE. E39372 (Fig. 8), herein selected from the three syntypes of *Zeuglopleurus rowei* Gregory. This specimen is from the Santonian of Westgate, Thanet Coast, Kent. The other two syntypes (now paralectotypes), 75556a and 75556b, are referred to the new subspecies *anglicus* (see p. 78; also p. 60).

OTHER MATERIAL. E39374-5 from the Santonian, *Uintracrinus* band of the Thanet Coast, Kent; E39804 from the Santonian, *Marsupites* band of south of High Stacks, Flamborough Head, Yorkshire; E39807 from the Lower Campanian, *quadratus* Zone, from a pit $\frac{1}{2}$ mile NW of Wells, Norfolk; GSM 118260 from the Santonian, *coranguinum* Zone, 0-0.5 m above Bedwell's Columnar Band, West Ramsgate, Thanet, Kent; GSM 11861-2 from the Santonian, mid-*Uintracrinus* Zone, at or just above level of *Hagenowia* horizon, Epple Bay, Birchington, Thanet, Kent; GSM 118263 from the Santonian, *coranguinum* Zone, 3.5-4 m below Bedwell's Columnar Band, West Ramsgate, Thanet, Kent; GSM 118264-5 from the Santonian, *coranguinum* Zone, in basal 0.5 m of Bedwell's Columnar Band, North Foreland, north of Broadstairs, Thanet, Kent. All GSM specimens are from the A. S. Gale collection.

PRESERVATION. The specimens are well preserved except for E39807 which is abraded and incomplete, and also partly enclosed in flint.

SHAPE (Figs 3a-f). The dimensions of the lectotype are: diameter of test 5.8 mm; height of test 3.9 mm; diameter of peristome 2.2 mm.

APICAL SYSTEM (Fig. 8d). 1) Ocular plates. Ornament consists of three large tubercles along the periproctal margin, and another near the margins next to interambulacral columns 1a and 4b. This tubercle is situated on a part of the plate anterior to the perradius. About three large tubercles are present along the adapical margins of oculars II-IV. These tubercles are very close together, forming a tall wall adapical to the ocular pore. All oculars are lightly sculptured between the tubercles.

2) Genital plates and madreporite. The ornament of genital plate 3 consists of several tubercles arranged in a circle around the genital pore, higher than the area of plate next to the periproct. The whole plate is lightly sculptured. The madreporic part of genital plate 2 covers most of the plate, and usually obscures the position of the genital pore by its perforations. On genital plate 5, two low, rounded ridges extend from the anterior limb of the 'boomerang' (see p. 65) to meet the raised rim around the genital pore. On the lectotype there are several thin striations extending from the plate margins next to the interambulacra towards the periproct; they are parallel with the anteroposterior axis on the adoral margin close to the interradius, and nearly parallel away from the interradius.

3) Periproct. The shape is approximately that of an elongated pentagon, with three shorter sides formed by the anterior parts of the periproctal margins of genital plates 1 and 4, and by all of the periproctal margins of genital plates 2 and 3. The two larger sides are formed by the posterior parts of the periproctal margins of genital plates 1 and 4, by all of the periproctal

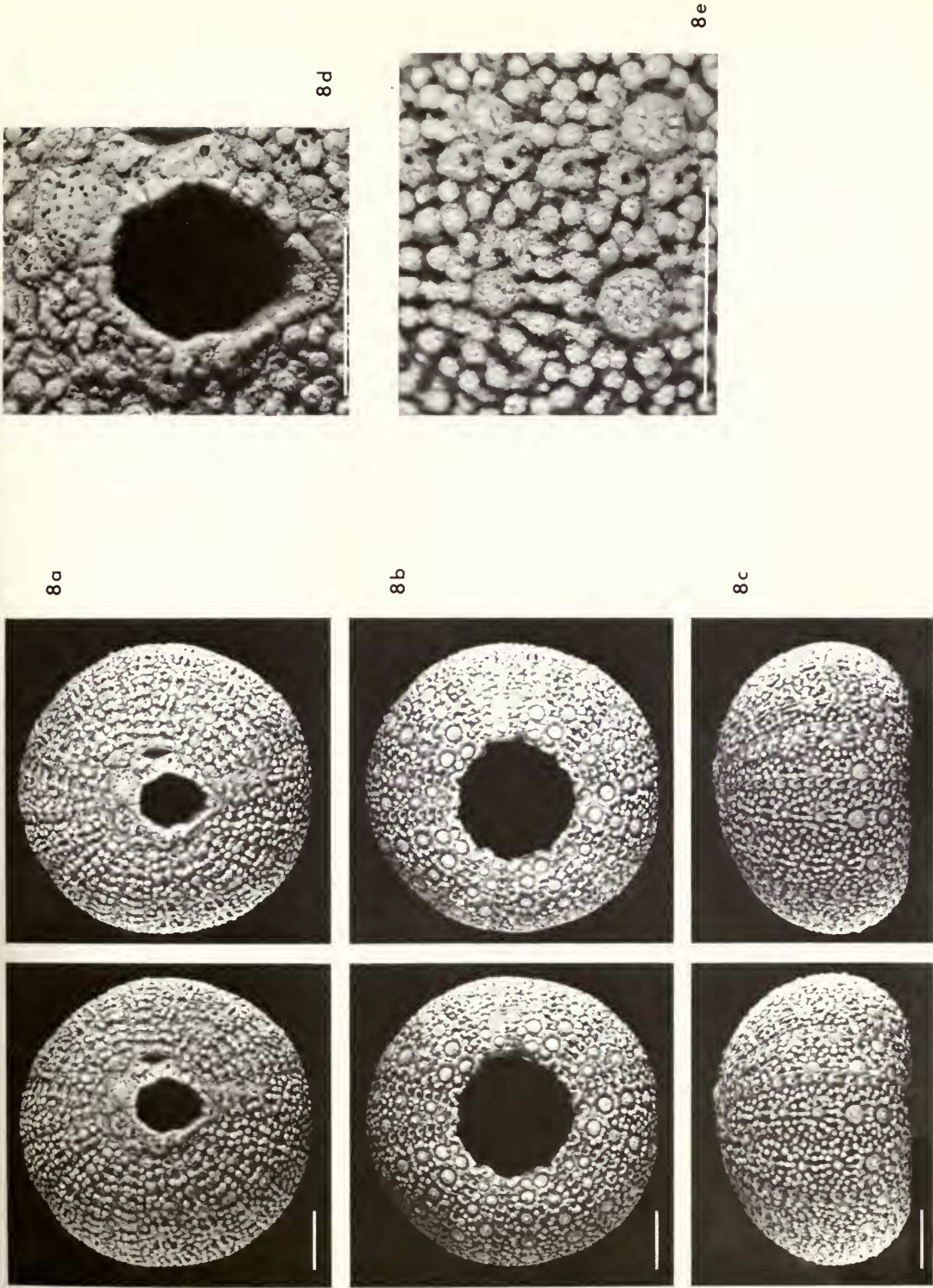


Fig. 8 *Boletechinus rowei rowei* (Gregory), lectotype E39372, herein selected. (a), stereo photograph of apical view; (b), stereo photograph of oral view; (c), stereo photograph of side view; (d), apical disc; (e), interambulacral ornament at the abrupt increase in size of tubercles, and part of an adjacent ambulacrum. Scale bars 1 mm.

margins of genital plate 5, and by ocular plates I and V. The periproct is about 25% longer than wide.

AMBULACRA. The ratios of the width of the ambulacra to the width of the interambulacra in the lectotype are: at the apical disc 1:1.6; at the ambitus 1:1.5; at the peristome 1:1.25. On the simple plates, the secondary tubercles occur singly at the perradial edge of the plate and also on the adapical adradial part of the plate, close to the pore-pairs of both simple and compound plates. The arrangement of the secondary tubercles together with the primary tubercles, and the shallow sculpturing, gives the appearance of two ribs per ambulacrum, extending from the apical disc to a position just adoral to the ambitus. The lack of sculpturing along the plate margins gives a uniform appearance to the ambulacra, with the individual plates indistinct.

INTERAMBULACRA (Fig. 8e). At the ambitus and adorally two secondary tubercles coalesce to form a ridge which extends from the adoral edge of a primary boss to two secondary tubercles of the next scrobicular circle. The other two tubercles are also in contact with the boss of the primary tubercle. Adapical to the ambitus there are up to four secondary tubercles extending from the adoral part of one primary boss to the adapical part of the next adoral primary boss. The effect of this arrangement is to produce two thin, discontinuous ribs along each column of interambulacral plates. Other secondary tubercles are situated quite close to each other and form rows which radiate from the primary tubercle to give a stellate appearance to the plate. Between all the secondary tubercles the test is lightly excavated to produce the spoked effect on the scrobicules. Lack of sculpturing along plate margins gives a uniform appearance to the ornament, with the boundaries of the individual plates indistinct.

PERISTOME (Fig. 8b). The auricles are short, angular and peg-like.

Boletechinus rowei (Gregory) *anglicus* subsp. nov.
Figs 2a, 3a-f, 9a-e, 10

1900 *Zeuglopleurus rowei* Gregory: 353-354, fig. 4.

1943 *Zeuglopleurus rowei* Gregory; Mortensen: 352-353.

DIAGNOSIS. A *Boletechinus* with plate margins well defined by sculpturing; secondary tubercles close together and confined within excavated areas; deep sculpturing between secondary tubercles; distinct excavated area usually present along the interradius, tapering adorally from apical disc to ambitus.

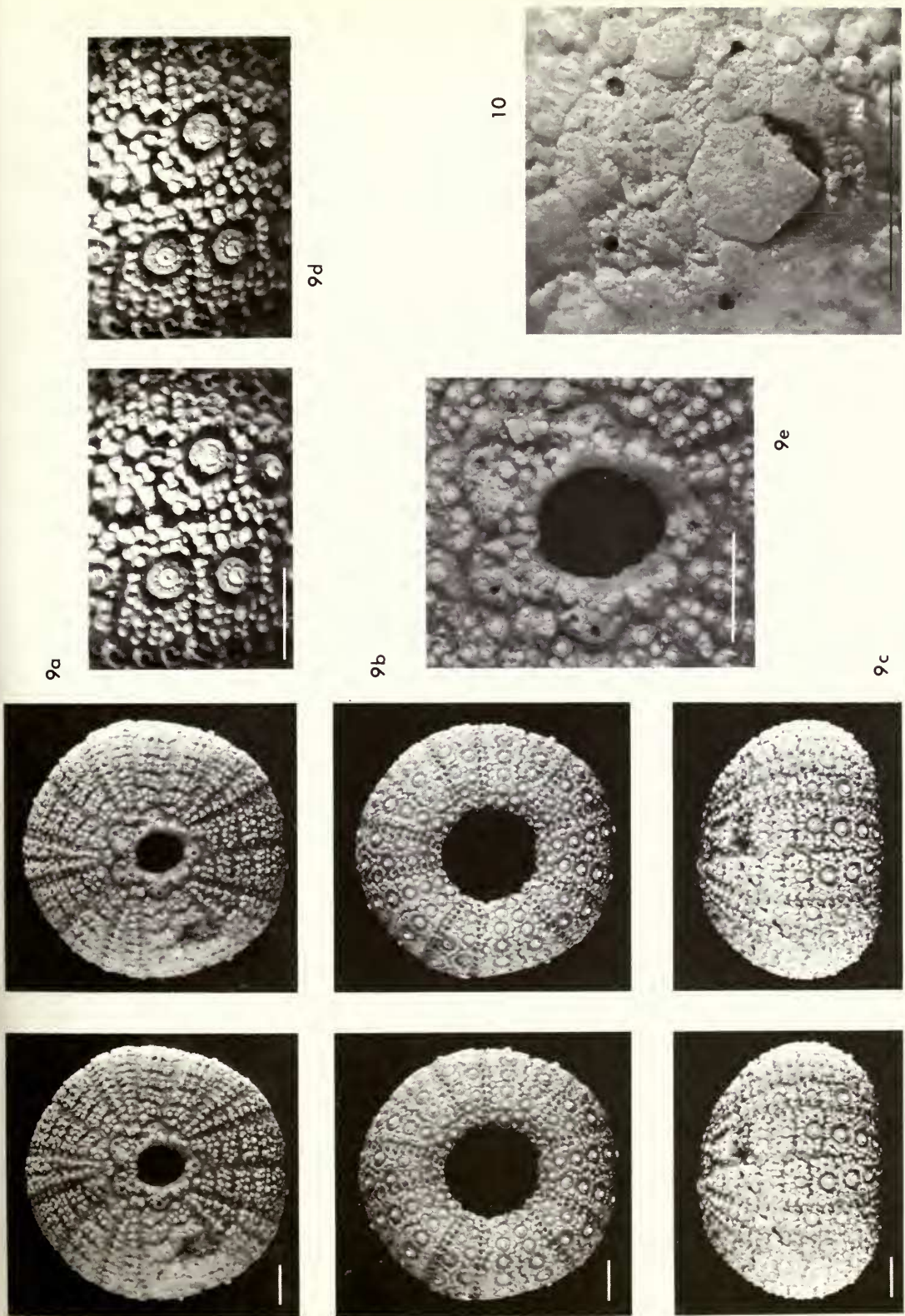
HOLOTYPE. BM(NH) 75556a (Fig. 9), a syntype of *Zeuglopleurus rowei* Gregory, from the Senonian of Charlton, Kent.

PARATYPES. BM(NH) 75556b, a syntype of *Zeuglopleurus rowei* Gregory, from the Senonian of Charlton, Kent; E39377-8 from the Santonian, base of *Marsupites* band, Thanet Coast, Kent; E39373 from the Santonian, base of the *Uintacrinus* band, Thanet Coast, Kent; E39805 from the same horizon at Flamborough Head, Yorkshire; E39376 from the Santonian, *Uintacrinus* band, Thanet Coast, Kent; GSM 118257 (Fig. 10) and 118258 from the Santonian, *coranguinum* Zone, 4.5 m above Whitaker's 3-inch band, Kingsgate, Thanet, Kent; GSM 118259 from the Santonian, *coranguinum* Zone, 0-0.5 m above Bedwell's Columnar Band, West Ramsgate, Thanet, Kent. All GSM specimens are from the A. S. Gale collection.

PRESERVATION. The specimens are all well preserved except for E39378 and E39376, which have been broken so that only parts of the tests remain.

SHAPE (Figs 3a-f). The dimensions of the holotype are: diameter of test 8.0 mm; height of test 5.6 mm; diameter of peristome 3.0 mm.

The holotype is a particularly large and fine specimen; a specimen of average size, such as E39377, has the following measurements: diameter of test 4.4 mm; height of test 2.9 mm; diameter of peristome 2.0 mm.



Figs 9–10 *Boletechinus rowei anglicus* subsp. nov. Fig. 9, holotype 75556a. (a), stereo photograph of side view; (b), stereo photograph of side view; (c), stereo photograph of side view; (d), stereo photograph of part of the interambulacral ornament; (e), apical disc. Fig. 10, GSM 118257. Apical disc of a small paratype, showing the periproctal plate in position. Scale bars 1 mm.

APICAL SYSTEM. 1) Ocular plates. The ornament consists of several tubercles developed close together, forming on oculars II–IV an approximately rectangular portion raised sharply above the general level of the plates. A raised part of oculars I and V forms an elongate ridge with three large tubercles. Each plate is strongly sculptured around the tubercles and margins.

2) Genital plates and madreporite. The ornament consists of small tubercles and swellings above the general level of the plates, and deep excavations between adjacent apical plates and between tubercles. On the holotype, along the margins between adjacent genital plates 2–4, the excavations are deeper than they are between genital plates 1 and 4 and oculars I and V. There are no excavations between genital plate 5 and oculars I and V. The genital pore of plate 2 is recognizable, and is usually situated on a low, more or less triangular-shaped portion of the plate, near the interradiial suture.

3) Periproct. The periproct has a scalloped appearance where the ornament of the component plates bulges into it. The periproct is about 15% longer than wide. The well-defined, raised ornament of all the component plates, except genital plate 5, forms a rim around the periproct. The lower ornament of plate 5 makes it almost level with the general surface of the test.

A single specimen (GSM 118257, Fig. 10) has preserved *in situ* a large, single anal plate which covers almost all of the periproct except for two small openings at ocular plates I and V. The plate fits closely to the periproctal margins of genital plates 1–4, but at the anterior ends of ocular plates I and V the margins of the anal plate are straight and extend directly to inter-radius 5 where they join at a point. Here the plate is not in close contact with genital plate 5. The two openings either side of the anal plate and periproctal margin are not the same size; the opening by ocular I is twice the size of the opening by ocular V. No other anal plates are preserved within the opening, so it is likely that the anus was protected by tiny plates on the anal integument.

AMBULACRA. The ratios of the width of the ambulacra to the width of the interambulacra of the holotype are: at the apical disc 1 : 2.5; at the ambitus 1 : 1.7; at the peristome 1 : 1.4. The holotype 75556a and paratype 75556b have both perforate and imperforate mamelons on the primary tubercles. Imperforate mamelons occur adapical to the ambitus; perforate mamelons occur at the ambitus and adorally, but only on the compound (diad) plates. In other respects the characters are those of *Boletechinus* type. Sculpturing of plates occurs along the perradiial margins of all plates, along the transverse margins of simple adapical plates, and around the individual secondary tubercles of the compound plates. Perradiial excavations taper adorally and are absent on the oral surface. The horizontal sutures of the oral surface are not sculptured. The sculpturing around plate boundaries makes the outline of the individual plates distinct.

INTERAMBULACRA. The holotype, and paratype 75556b, have perforate mamelons from the ambitus adorally. Secondary tubercles form contiguous scrobicular circles and up to three other incomplete circles with occasional extra tubercles along the perradiial margin of the plate. The scrobicular area is well defined on larger primary tubercles because the secondary tubercles are further from the primary boss than they are on smaller primary tubercles. The sculpturing of the interambulacra is present along the horizontal margins of plates adapical to the ambitus, where it follows the outline of the secondary tubercles. Distinct sculpturing also occurs along the interradiial margins, again following the outline of the tubercles. This sculpturing is a wide excavation adapically and tapers to a very thin excavation near the peristome (Fig. 9d). However, the excavation of the interradiial area is not well developed in all specimens.

The horizontal sutures are also 'divided' by a single or by two short, low, radiating ridges which extend from an adapical primary boss to the adoral scrobicular tubercles. These ridges are best developed at the ambitus adapically. From the ambitus adorally, ridges are less well developed and contiguous scrobicular tubercles only occur, to separate one plate from the next. Sculpturing between adapical plates and adoral plates from the ambitus adorally becomes less distinct, until it is hardly present at all on the oral surface. The sculpturing along the adradial suture follows the outline of the secondary tubercles and the tilted part of adjacent ambulacral plates, to give a notched appearance.

PERISTOME. The auricles are short, broad, leaf-shaped prongs with a 'keyhole'-shaped space between the prongs of a pair.

NOTES ON THE PERFORATION OF THE TUBERCLES. Although the primary tubercles of the holotype 75556a and the paratype 75556b, from ambitus adorally, are perforate, the perforations are quite small and were overlooked by Gregory (1900). None of the other specimens of either *B. r. rowei* or *B. r. anglicus*, nor any of the American specimens, have perforate tubercles. Perforations in the primary tubercles of *Tylocidaris* can be found in the most adapical interambulacral plates, which show a secondary loss of perforation (see Lewis & Ensom 1982: 102), but the retention in *B. r. anglicus* of perforations from the oral surface to the ambitus in specimens of greatly differing sizes—75556a is 8 mm in diameter, 75556b is 4.2 mm in diameter—is puzzling.

Genus *ZEUGLOPLEURUS* Gregory 1889

TYPE SPECIES. *Zeuglopleurus costulatus* Gregory 1889.

DESCRIPTION¹. *Shape:* A small regular echinoid with an approximately hemispherical test, with the anterior end slightly higher than the posterior end.

Apical System: 1) Ocular plates I and V are insert. All the oculars have M-shaped margins next to their ambulacra. The ornament consists of tubercles and excavations.

2) Genital plates and madreporite. These form the anterior, lateral and posterior-most margins of the periproct. Genital plate 5 is smaller than the other four genital plates, has no distinct swelling into the periproct, and has a central pore. The other genital pores are slightly perradial in position, towards the anterior paired ambulacra. The madreporite is slightly raised and has many small pores. The ornament of the plates consists of small tubercles, granules and excavations, except for plate 5 which has no ornament.

3) Periproct. The boundary composed of ocular plates I and V and genital plates 1–4 may be raised as a rim, whilst the boundary composed of genital plate 5 remains flush with the test. The periproct is slightly elongated anteroposteriorly.

Ambulacra: These are straight, and taper adapically and adorally and are widest at the ambitus. The pore-pairs are arranged in monoserial columns and are oblique, with the adradial pore more adapical than the perradial pore. The first few plates from the apical disc adorally are simple; they then become compounded in the acrosaleniid manner. The ornament consists of primary and secondary tubercles and sculpturing and excavation of the test.

The primary tubercles each have a low, convex, crenulated boss, and a large, imperforate hemispherical mamelon with an undercut neck. Scrobicules are also present.

Secondary tubercles have low, convex bosses and small hemispherical mamelons. They form scrobicular circles and occupy other areas of the plates.

Sculpturing consists of excavations along sutures and around secondary tubercles, and is best represented adapically to the ambitus. Adorally from the ambitus the sculpturing is reduced.

Interambulacra: These taper adorally and adapically and are widest at the ambitus. The ornament is similar to that of the ambulacra. The tubercles of both interambulacra and ambulacra increase in size steadily to the ambitus, then decrease steadily.

Peristome: This is decagonal and is slightly elongated anteroposteriorly. The gill-slits are shallow.

RANGE. Upper Cretaceous of Europe.

Zeuglopleurus costulatus Gregory

Figs 2a, 3a–f, 11a–e

1889 *Zeuglopleurus costulatus* Gregory: 495–496, figs 1–5.

1889 *Zeuglopleurus costulatus* Gregory; Duncan: 103.

1911 *Zeuglopleurus costulatus* Gregory; Lambert & Thiéry: 217.

¹ See also the diagnosis by Gregory, 1889.

1935 *Zeuglopleurus costulatus* Gregory; Lambert & Jeannot: 6.

1943 *Zeuglopleurus costulatus* Gregory; Mortensen: 352–353, text-figs 211a–d, 212, 213.

DIAGNOSIS. Test slightly flattened posteriorly; apical disc fairly large; periproct slightly elongate and slightly posterior; peristome of moderate size, slightly elongated anteroposteriorly; ornament includes deep excavations and adapical–adoral ridges connecting adjacent plates and radiating ridges on scrobicules.

HOLOTYPE. BM(NH) E4365 (Fig. 11), from the Cenomanian, Chalk Marl, *varians* Zone, of Glynde, near Lewes, Sussex. All measurements referred to in the description are those of the holotype.

OTHER MATERIAL. E39790–3, E79244, from the Turonian, *cuvieri* Zone from the south Devon coast. All the material is in the collections of the BM(NH), Department of Palaeontology.

PRESERVATION. The type specimen is well preserved, uncrushed and has most of its tubercles intact except for those of the oral surface. These are slightly abraded. The specimens from Devon have all lost their ocular and genital plates; one specimen—E39792—is crushed, and others of the group have incomplete tests.

SHAPE. The holotype is approximately hemispherical, with the anterior end slightly higher than the posterior end. The peristome is elongated anteroposteriorly and is of moderate size. The periproct has the outline of an inverted comma, and has a raised rim except at genital plate 5.

Table 4 Dimensions (mm) of the holotype E4365 of *Zeuglopleurus costulatus* Gregory.

	Diameter of test	Height of test	Diameter of peristome	Diameter of apical disc
Post.-Ant.	11.0	6	4.4	5.0 (III–5)
Lateral	10.75		3.8	4.0 (4–1)

APICAL SYSTEM (Fig. 11d). 1) Ocular plates. Ocular plates I and V are about 25% longer than oculars II, III and IV, and all have irregular outlines and concave periproctal margins. Oculars II, III and IV all have six sides.

The ornament of all the oculars consists of many small tubercles very close together, giving a swollen appearance to the plates. Oculars I and V have a wide, smooth rim adjacent to the periproct. At each M-shaped margin the plate is deeply excavated, and has a tiny, diamond-shaped area with minute granules on the surface. The ocular pore is obscured.

2) Genital plates and madreporite. Genital plates 1, 2, 3 and 4 form the anterior and lateral margins of the periproct. The periproctal margins of plates 2, 3 and 4 are gently concave; that of plate 1 has a convex bulge along the anterior two-thirds and extends downwards and obliquely to the vertical margin of genital plate 2 (see Fig. 11d). The bulge may possibly be a single periproctal plate which has remained in position *post mortem*, but the suture between it and the rest of plate 1 cannot be seen. It is this bulge which gives the periproct its comma shape. The periproctal margins of plates 1 and 4 are about twice as long as those of 2 and 3.

Genital plate 5 is considerably smaller than the others and forms part of the posterior rim of the periproct.

The ornament of the genital plates consists of very small tubercles and granules randomly distributed over the surface. In between the tubercles there are deep, circular or elongated excavations, except between the tubercles of plate 5. The madreporite has an approximately circular outline, and with many small perforations over the surface. The genital pore of plates 3 and 5 is interradianal in position. The pore is situated near the adoral side of plates 1–4, and centrally in plate 5, and is slightly elongated in the direction of the interradianus.

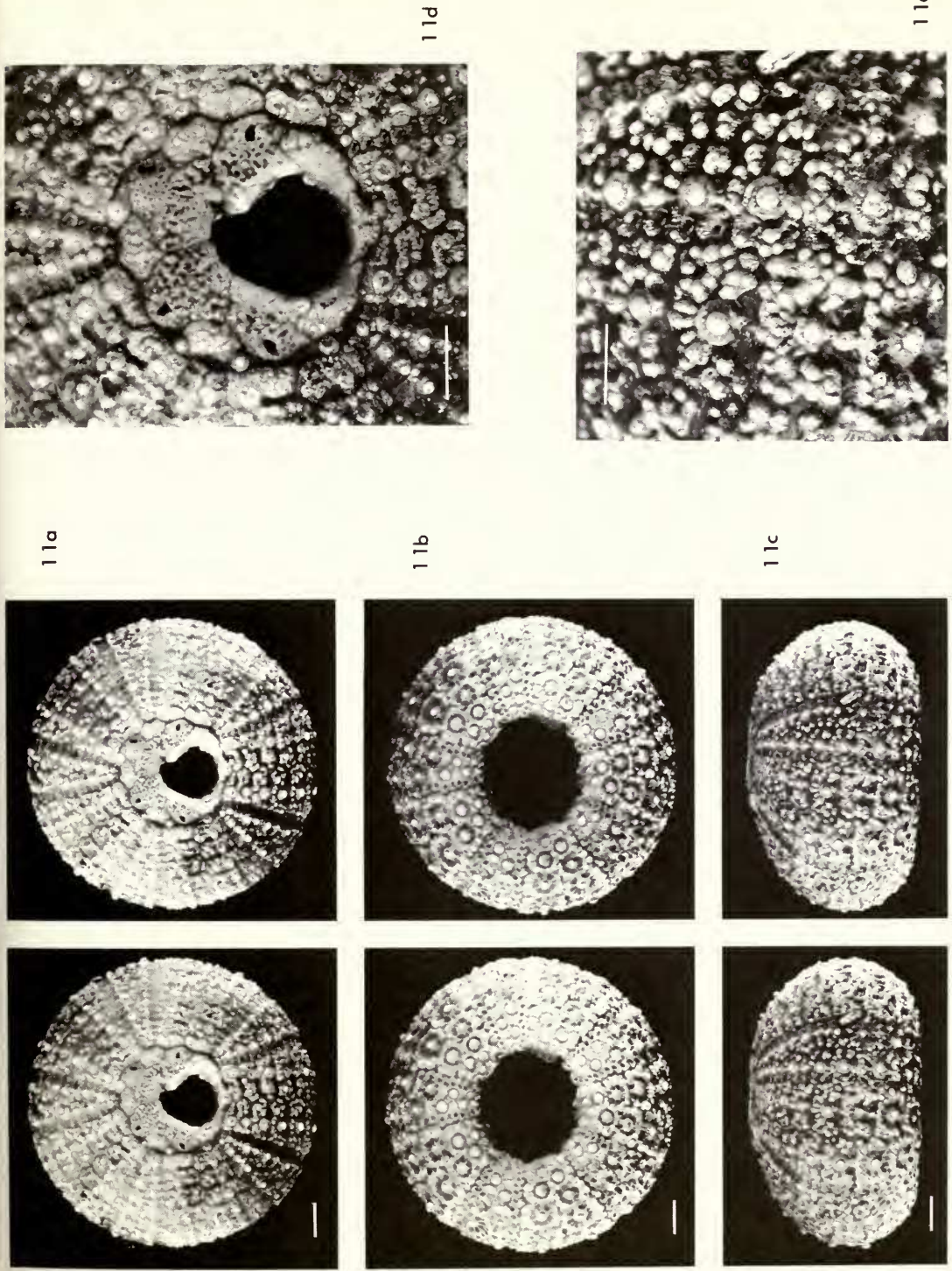


Fig. 11 *Zeuglopleurus costulatus* Gregory, holotype E4365. (a), stereo photograph of apical view; (b), stereo photograph of oral view; (c), stereo photograph of side view; (d), apical disc; (e), ambulacral and interambulacral ornament. Scale bars 1 mm.

The periproctal margins of genital plates 2, 3 and 4 are angular, whilst those of plates 1 and 5 are rounded, with the smooth inner surface of the periproctal margin extending for a short distance over the outer edge of the plates.

Table 5 Dimensions of genital plates in holotype of *Zeuglopleurus costulatus* Gregory. L = maximum length between adradial margins; W = maximum width, periproctal margin to interradiial suture (mm).

Plate	L	W
1	1.2	1.2
2	1.35	1.3
3	1.2	1.25
4	1.15	1.1
5	1.05	0.5

3) Periproct. The outline of the periproct is comma-shaped, possibly because of an included periproctal plate. The longest dimension along the anteroposterior axis is about 2.2 mm, and the widest part of the 'comma' measures about 2.0 mm. The periproctal border is smooth and has no ornament on genital plates 1, 4 and 5 and oculars I and V. The ornament of genital plates 2 and 3 extends to the periproct. The border is raised as a rim above the general level of the test, slightly lower at the anterior end and much lower at the posterior end. The adradial ends of oculars I and V and all of genital plate 5 are at the same lower level.

AMBULACRA (Fig. 11e). These are straight, taper adorally, adapically, and are widest at the ambitus. The ratios of the width of the ambulacra to the width of the interambulacra are:

at the apical disc 1 : 3.3
at the ambitus 1 : 1.5
at the peristome 1 : 1.3

The simple plates are the two to five most adapical plates, followed by compound plates of acrosaleniid type. There are some diads adapical to the ambitus which are present between acrosaleniid compound plates.

Table 6 Number of plates in each ambulacral column in holotype of *Zeuglopleurus costulatus* Gregory.

	Ia	Ib	IIa	IIb	IIIa	IIIb	IVa	IVb	Va	Vb
Simple	2	3	5	4	2	3	2	2	2	4
Diads	4	1	1	0	2	2	4	3	0	0
Triads	5	7	7	8	8	7	6	7	9	8

The pore pairs are small, oblique and very slightly elongated, with the long axis of the adradial pore parallel to the transverse sutures and the long axis of the perradial pore adapical-perradial adradial-adoral. The pores are slightly sunken into a lobed part of the plate, with the margin of the perradial pore open at a narrow gap on the adoral side. The pores are situated in the adoral perradial 'corner' of the lobe, and are separated from each other by a fairly wide wall.

The ornament of the ambulacra consists of large primary tubercles, small secondary tubercles and tiny ridge-like and teardrop-shaped granulations, and deep excavations along sutures and around tubercles.

Each primary tubercle has up to about thirteen small crenulations. Scrobicules are present on the compound plates, narrow on the diads and wide on the others. The wide scrobicules have eight or nine thick radiating ridges extending radially from the primary boss to the scrobicular tubercles.

The ridge and teardrop granulations are very small—a typical teardrop is 0.1 mm long, a ridge is 0.14 mm long. Their long axes are parallel to the perradius; the ridges are arranged side-by-side, while the teardrops alternate with each other and interlock.

The primary tubercles form two columns in each ambulacrum. The simple plates have a tubercle in the centre, the diad compound plates have the adoral tubercle overlapping the adapical plate, the acrosaleniid compound plates have the large tubercle in the centre of the two adapical plates and the third simple plate has a very small primary tubercle of the same size as the secondary tubercles.

The secondary tubercles form incomplete scrobicular circles and are present on all plates except the most adapical ones. The adapical diad compound plates have only one or two along the perradial part of the plate, but those nearer to the ambitus have more secondary tubercles, up to four of them, along the perradial margin. The acrosaleniid compound plates have secondary tubercles along the adapical edge, perradial edge and adoral edge of the plate. The simple plate between adjacent compound plates shares its secondary tubercles so that there is a 'clumping' of tubercles between the compound plates. There is usually a single secondary tubercle, or a scrobicular ridge, between adjacent adoral and adapical plates, which is in close contact with the boss and which together with the primary tubercle forms two discontinuous but prominent ridges down each ambulacrum from the apical disc to the ambitus. From the ambitus adorally the ridges are insignificant. On the oral surface the scrobicules become much narrower, concomitant with the reduction in size of the plates, and the ornament is simplified.

On a few compound plates a single tubercle occurs on the adradial adapical part of the lobe which bears the pore pair.

The granulations are best developed on the adapical side of the lobe of the pore-pairs, but less developed ones are also present on the secondary tubercles along the perradial sutures. The deep sculpturing is mostly confined to the area of the test between apical disc and ambitus, and is represented by deep excavations along sutures and around secondary tubercles. The secondary tubercles are undercut on the adapical edges of the plate. Adoral to the ambitus the excavations are much reduced and are very weak along the adradial sutures.

INTERAMBULACRA (Fig. 11e). The ratios of the width of an interambulacrum at the peristome, the ambitus and the apical disc are: 1.5 : 2.5 : 1.

The ornament is similar to that of the ambulacra. Each primary tubercle has a small convex boss which is elongated at its adoral side into a single or forked ridge. The boss has about fifteen small crenulations and a very narrow platform.

The primary tubercles are situated in the middle of the plates, and secondary tubercles are present on the adapical, adradial and interrarial parts of each plate, but not on the adoral parts. The secondary tubercles form approximately semicircular scrobicular arcs around the primary tubercles—slightly less than semicircular nearer the apical disc to slightly more than semicircular at the ambitus and adorally. There are also up to two additional arcs of secondary tubercles present on the adradial and interrarial margins of the plates, except on plates immediately next to the peristome where only one semicircle of tubercles is present. There are thick ridges extending radially from the base of the primary boss to adjacent secondary tubercles. On plates at the ambitus and adoral to it, the secondary tubercles are raised to the same level as the primary mamelon. On the adoral edge of the plate there is one thick ridge from the primary boss to the adapical scrobicular semicircle of the adjacent adoral plate. This ridge is very thick adapically, but adorally, towards the ambitus and adoral to the ambitus, the ridge bifurcates into a narrow, inverted V-shape. These ridges, together with the primary tubercles, give an appearance of two discontinuous ribs down the interambulacrum to the oral surface, where they cease.

The granulations are similar to the ridge type found on the ambulacra, but are much less

pronounced and less extensive. They are present at the adradial and interradial sides of the plates. The sculpturing is very wide and fairly deep, and slightly undercuts the adapical edges of the scrobicular semicircles. The excavations are approximately triangular areas either side of the thickened and bifurcated ridges. Other excavations are present around the secondary tubercles along interradial and adradial margins. The sculpturing and excavations are much reduced or absent on the oral surface.

There are between 10 and 12 plates in each interambulacral column.

PERISTOME (Fig. 11b). This is slightly elongated anteroposteriorly, and has shallow but distinct gill slits. The gill slits have a narrow rim which is continuous from one slit, across the oral extremity of the interambulacrum to the other slit. The inside of the test of the holotype has some matrix remaining, and a small calcareous overgrowth which has extended into the peristome. However, the apophyses are visible as low, robust structures, and the auricles of Ia, Ib, IIa, IIIa, IIIb, IVa, IVb, Vb are also present, forming short peg-like structures, unjoined in the middle.

Comparisons between *Boletechinus*, *Zeuglopleurus*, and other genera

Boletechinus delawaricus differs from *B. mcglameryae* in its ornament, in the less abrupt increase in size of its primary tubercles, and in the shape of the genital plates. The ornament of *B. delawaricus* has a less granular appearance than that of *B. mcglameryae*; the ridges enclosing the diamond-shaped depressions between adjacent interambulacral plates of *B. delawaricus* are represented in *B. mcglameryae* by two almost parallel ridges. Genital plate 5 of *B. mcglameryae* is elongated adorally almost to a sharp point, with the narrow width accentuating the point, whereas in *B. delawaricus* the plate is not elongated into a point; the width is much greater than the length, so that the sharp point is not produced. The apical disc of *B. delawaricus* is more elongate and has an oval outline whilst that of *B. mcglameryae* is angular. The diameter of the peristome of *B. delawaricus* is between 42% and 44% of the diameter of the test (mean 43%), whilst the diameter of the peristome of *B. mcglameryae* is between 33% and 41% of the diameter of the test (mean 37%; Cooke (1955) says '... nearly one third . . .'): see Fig. 3e, p. 67.

Boletechinus r. rowei differs from *B. mcglameryae* by having a stellate arrangement of secondary tubercles on the interambulacral plates. The plate boundaries of *B. r. rowei* are much less well defined than are those of *B. delawaricus*. The most obvious difference between the two subspecies of *B. rowei* is the much stronger sculpturing present on *B. r. anglicus*, especially around the plate margins. The boundaries of the plates of *B. r. anglicus* are quite distinct, whereas those of *B. r. rowei* are indistinct, giving the test a much more uniform appearance in its tuberculation. The interradial excavation on many specimens of *B. r. anglicus* assists further in their distinction. In other respects the two subspecies are difficult to separate. The sculpturing of the test of *B. r. anglicus* is very similar to that of *Z. costulatus*, so that Gregory (1889) regarded specimens 75556a and b—the holotype and a paratype of *B. r. anglicus*—as juveniles of *Zeuglopleurus costulatus* in his original descriptions. He later changed his mind and in 1900 placed these supposed 'juveniles' with *Z. rowei*. However, the abrupt increase in the size of the primary tubercles at the ambitus of the *Boletechinus* easily distinguishes *B. r. anglicus* from *Z. costulatus*.

Glyptocyphus difficilis may be distinguished from *Zeuglopleurus costulatus* by having irregularly developed ambulacral plate-compounding. *G. difficilis* frequently has groups of compound ambulacral plates which have no enlarged primary tubercles. The compounding is acrosaleniid but is also irregularly developed. *Z. costulatus* has a more regularly developed acrosaleniid compounding.

Echinocyphus tenuistriatus differs from *Z. costulatus* in its different ornament, which consists of a broad inverted V-shaped excavation along the adoral edge of the plates. The secondary tubercles are smaller and more widely separated than those of *Z. costulatus*. Although the difference between these two species is evident, *Echinocyphus* and *Zeuglopleurus* may yet prove to be congeneric; however, the discussion of this lies outside the scope of the present paper.

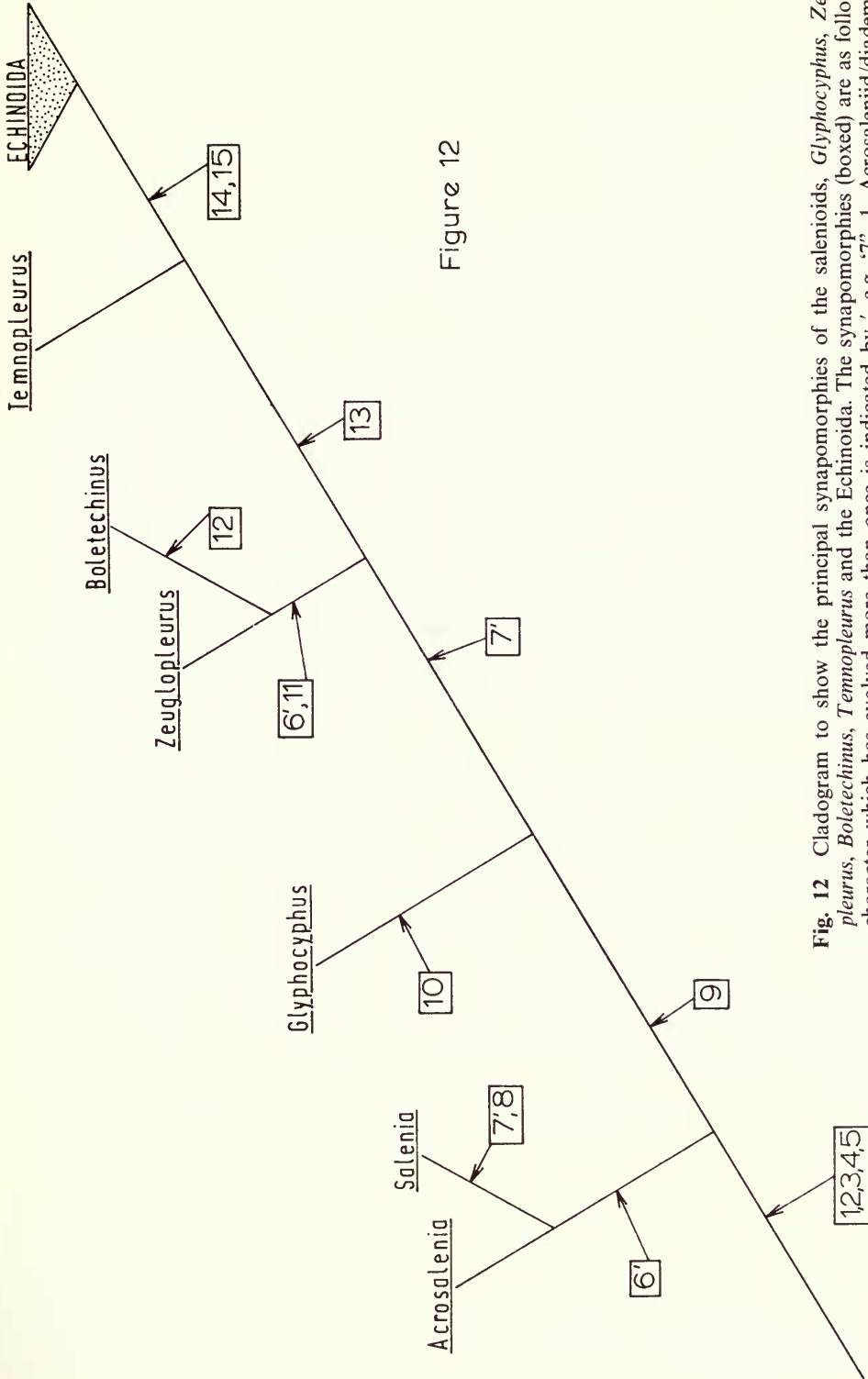


Figure 12

Fig. 12 Cladogram to show the principal synapomorphies of the salenioids, *Glyphocyphus*, *Zeuglopleurus*, *Boletechinus*, *Temnopleurus* and the Echinoidea. The synapomorphies (boxed) are as follows; a character which has evolved more than once is indicated by ', e.g. '7'. 1, Acrosaleniid/diadematoid compounding; 2, Perforate tubercles; 3, Crenulate tubercles; 4, Tubercle size increase gradual to ambitus; 5, Dicyclic disc; 6, Large suranal plate(s) retained in adults; 7, Tubercles imperforate; 8, Single suranal plate tessellated into disc; 9, Sculptured test; 10, Monocyclic disc; 11, Oculars I and V insert; 12, Abrupt increase in size of tubercles at ambitus; 13, Echinoid compounding; 14, Loss of test sculpturing; 15, Loss of tubercle crenulation.

Species of *Zeuglopleurus* other than *Z. costulatus* are recorded from Europe, and include *Z. colleti* (Turonian of France) which has straight pore-pairs, and sculpturing of the horizontal sutures similar to those of *Z. costulatus* but elsewhere not so extensive. Mortensen (1943: 353) reported that a specimen he examined by grinding down the test showed '... the echinoid type of ambulacra ...', unlike the acrosaleniid type of *Z. costulatus*.

Z. glanoviensis Kongiel 1939 (Turonian of Poland) is flattened adorally and adapically, and has unigeminate ambulacra with compound plates '... almost unfused ...'.

Z. pusillus (Roemer 1840) (Cretaceous of Germany) has a flattened oral surface and a circular periproct, but other details of structure and ornament cannot be seen in the figures of Roemer, and his descriptions are inadequate.

Z. (?) cannabis (Desor 1858) is imperfectly known as Desor did not give a figure. Gregory (1889) regarded it as probably a *Zeuglopleurus*, differing from *Z. costulatus* in that '... the tubercles are less conjugate; the apical system is also less annular ...'.

Stratigraphical distribution of *Boletechinus* and *Zeuglopleurus*

Stratigraphical details supplied with the specimens in the Rowe collection, BM(NH) and with specimens in the collections of A. S. Gale, GSM, show that the two species of *Boletechinus* from England are at present confined to the Santonian and Campanian. The majority of specimens of *B. r. rowei* in the Gale collections come from around Bedwell's Columnar Band, *Micraster coranguinum* Zone, and two others from the middle *Uintacrinus* Zone of the Santonian. Specimens of *B. r. rowei* in the Rowe collections are recorded from the *quadratus* Zone of the Campanian and the *Marsupites* and *Uintacrinus* Zones of the Santonian.

Specimens of *B. r. anglicus* in the Gale collections come from Whitaker's 3-inch band, *M. coranguinum* Zone, and from about 0.5 m above Bedwell's Columnar Band (see Rowe 1900: 289–367). Specimens in the Rowe collections come from the *Marsupites* and *Uintacrinus* Zones.

The two American species of *Boletechinus* are from the Maastrichtian.

Table 7 Summary of distribution of *Boletechinus* and *Zeuglopleurus* species.

	Cenomanian	Turonian	Coniacian	Senonian			Campanian	Maastrichtian
				<i>coranguinum</i> Zone	<i>Uintacrinus</i> Zone	<i>Marsupites</i> Zone		
<i>B. mcglameryae</i>	-	-	-	-	-	-	-	X
<i>B. delawaricus</i>	-	-	-	-	-	-	-	X
<i>B. r. rowei</i>	-	-	-	X	X	X	X	-
<i>B. r. anglicus</i>	-	-	-	X	X	X	-	-
<i>Z. colleti</i>	-	X	-	-	-	-	-	-
<i>Z. glanoviensis</i>	-	X	-	-	-	-	-	-
<i>Z. costulatus</i>	X	X	-	-	-	-	-	-

Species of *Zeuglopleurus* are known from the Cenomanian and Turonian. *Z. costulatus* comes from the *varians* Zone of the Cenomanian and the *cuvieri* Zone of the Turonian, and *Z. colleti* and *Z. glanoviensis* are said in their descriptions to come from the Turonian. Age details of other species of *Zeuglopleurus* are not given in their descriptions.

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